PREDATOR-MEDIATED HABITAT USE BY JUVENILE WHITE HAKE (*Urophycis tenuis*) AND GREENLAND COD (*Gadus ogac*)

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PREDATOR-MEDIATED HABITAT USE BY JUVENILE WHITE HAKE (*Urophycis tenuis*) AND GREENLAND COD (*Gadus ogac*)

by

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ABSTRACT

Juvenile white hake (*Urophycis tenuis*) abundance has been increasing on the northeast coast of Newfoundland over the past two decades. In these coastal areas juvenile white hake and Greenland cod (*Gadus ogac*) overlap spatially and temporally in eelgrass (*Zostera marina*) habitat, an important nursery for young of the year gadids. Concern has arisen that the recent increase in white hake abundance may be negatively impacting other gadids, such as Greenland cod. The purpose of my study was, therefore, to investigate the habitat use and behavioural interactions of juvenile white hake and Greenland cod and how this may vary in response to predator threat (an age 3+ Atlantic cod; *G. morhua*) and interspecific competition. A series of laboratory experiments were undertaken to determine habitat use under these different scenarios by dividing the bottom of two replicate arenas (2 x 2 x 0.5 m) into thirds and covering these with artificial eelgrass, cobble, or sand. My study documented overlapping habitat use by juvenile white hake and Greenland cod and supported the contention that eelgrass serves as an important refuge habitat for both species, with Greenland cod showing the highest affinity. Furthermore, interspecific competition experiments showed evidence of white hake excluding Greenland cod from preferred habitat as a result of competition for refuges. The size advantage that white hake gain over Greenland cod early during demersal life may be the main mechanism that influences the outcome of this habitat competition.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1

General Introduction

1.1 Natural Mortality

Predation is a main cause of natural mortality during the early life stages of fish (Crowder 1980, Hunter 1981, Lima and Dill 1990, Sogard 1997). By decreasing predation risk, fish can increase survival probability and ultimately their fitness within existing trait tradeoffs (e.g., with foraging; Lima and Dill 1990). One common anti-predator behaviour is predator avoidance (Sih 1979, Sih et al. 1998).

1.2 Predator Detection and Avoidance Behaviours

Predator detection initially occurs when a prey senses a predator's presence. Potential prey can detect cues through visual, auditory, or chemosensory means, as well as through changes in the behaviour of other nearby prey which have detected such cues (Pitcher and Parrish 1993). Predator detection usually leads to defensive or anti-predatory behaviours (Pitcher and Parrish 1993). One such behaviour that dominates the survival instinct of potential prey is avoidance.

Potential prey use avoidance behaviours as a method to evade detection by predators (Sih 1987). Staying out of the predator's sensory field can be accomplished by maximizing distance from predators and reducing activity during predator presence (Howick and O'Brien 1983, Sih 1987). Furthermore, some non-cryptic preys alter their activities spatially and temporally to places and times where and when predators are absent (Sih 1987).

Prey commonly use crypsis to avoid detection by a predator when in close proximity (Sih 1987). Lough et al. (1989) found that juvenile Atlantic cod (*Gadus*

morhua) and haddock (*Melanogrammus aeglefinus*) on eastern Georges Bank, in the offshore area of the Atlantic Ocean, can use cryptic coloration to blend in with fine grained substrates as a predator avoidance strategy. Furthermore, Gregory and Anderson (1997) demonstrated this strategy for young Atlantic cod in coastal Newfoundland.

Additionally, some prey may escape predator detection by using a motionless strategy (Gotceitas and Colgan 1987, Savino and Stein 1989). For example, juvenile bluegill sunfish (*Lepomis macrochirus*) adopt a motionless behaviour in response to exposure to largemouth bass (*Micropterus salmoides*). Bass usually ignored sunfish when they were motionless (Gotceitas and Colgan 1987). Evading predator detection by using a motionless behaviour can be extremely effective when coupled with cryptic coloration.

1.3 Habitat Complexity

Predation risk also influences habitat selection by prey (reviewed by Lima and Dill 1990). Habitat selection is defined as the behavioural responses and environmental factors that lead to preference of one habitat over another (Meadows and Campbell 1972). In aquatic environments, structurally complex habitats are ideal because they reduce the foraging abilities of piscivores (Savino and Stein 1982, Gotceitas and Colgan 1989, Matilla 1992, Persson and Eklov 1995), resulting in less predation risk for the juvenile fish that use these habitat types for refuge (Savino and Stein 1982, Werner et al. 1983a, b, Orth et al. 1984, Mittelbach 1986, Gotceitas and Colgan 1989, Gotceitas and Brown 1993, Gotceitas et al. 1995, Persson and Eklov 1995, Tupper and Boutilier 1995a, Gotceitas et al. 1997, Rangeley and Kramer 1998,

Linehan et al. 2001, Heck et al. 2003, Laurel et al. 2003a). In particular, complex structure can reduce vision and swimming abilitities of piscivores (Gotceitas and Colgan 1989, Savino and Stein 1989) and provide hiding places for younger fish (Gregory and Anderson 1997).

Structurally complex habitats that enhance juvenile fish survival in the northwest Atlantic Ocean include vegetation (eg. Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003a) and cobble substrates (eg. Gotceitas and Brown 1993, Gotceitas et al. 1995, Tupper and Boutilier 1995a, Fraser et al. 1996). Tupper and Boutilier (1995a) suggested that juvenile Atlantic cod survival and densities were higher in structurally complex habitats. Seagrass provided a greater opportunity for growth, while cobble resulted in a higher survival probability. Moreover, Laurel et al. (2003b) found that predation rates on juvenile Atlantic cod are higher in habitats lacking structural complexity.

1.4 Juvenile Fish Growth and Survival

In addition to providing refuges for juvenile fish to hide in, structurally complex habitats usually contain higher densities of food (Orth et al. 1984), which results in enhanced growth rates for inhabitants (Crowder and Cooper 1982, Tupper and Boutilier 1995a, Heck et al. 2003). Based on optimization theory, fish should select habitats that maximize their foraging success in the face of predation risk (Sogard 1994). In habitats where the ratio of mortality to growth rates is minimized, fitness is maximized (Gilliam 1982). Fitness is maximized because individuals gain size at low risk of mortality (Rowe and Ludwig 1991).

Prey selectivity is dependent on size, density, habitat, and mobility (Zhao et al. 2006). During the larval and juvenile stages, the smallest individuals are usually the most vulnerable to predation (eg. Parker 1971, Folkvord and Hunter 1986, Post and Evans 1989, Luecke et al. 1990). At a predator-prey length ratio greater than 15 to 1 the probability of escaping predation is almost zero (Miller et al. 1988). Typically, the minimum predator-prey length ratio for piscivores is 2:1 (Power 1987, Miller et al. 1988), whereas average predator-prey length ratio is usually 5-10 to 1 (Power 1987).

In general, survival increases with increasing size (Peterson and Wroblewski 1984, Houde 1987, Miller et al. 1988, Milinski 1993) because larger individuals can better escape predation, resist starvation, and cope with physiological constraints (Sogard 1997). Therefore, rapidly growing individuals should be favoured because they spend less time at a vulnerable size; reaching size refuges from natural mortality factors, such as cannibalism and predation more quickly (Sogard 1997). In addition, faster growing individuals can reach larger sizes at an earlier age, which can also result in increased reproductive success (Werner and Gilliam 1984, Magnhagen and Kvarnemo 1989, Buckley et al. 1991).

Although, smaller fish usually experience greater mortality, this is not always true. Optimal foraging theory predicts that predators select prey with the highest energetic return (Werner and Hall 1974, Savino and Stein 1982). Larger prey have a higher energetic return when they are easily captured. Moreover, rapid growth and increased size are accompanied by increased activity, which can lead to heightened predation risk. Furthermore, Pratt and Fox (2002) actually showed that risk of over-

winter morality for juvenile walleye (*Sander vitreus*) was related to size. Small walleye gained more weight and lost less energy than larger walleye in ponds with and without predators.

1.5 Density-Dependent Effects

In years where high densities of juvenile fish settle to demersal habitats, available structure for use as a refuge could exceed carrying capacity and potentially become limited (Johnson et al. 1988, Laurel et al. 2004, Blanchard et al. 2005). Density-dependent habitat selection is one explanation for why fish may be forced to use suboptimal or "high risk" habitats (Laurel et al. 2004, Blanchard et al. 2005). For example, juvenile Atlantic cod may compete for refuge from predation and at a certain density threshold it is possible that competition for a limited amount of shelter might lead to juvenile cod population regulation, with high levels of mortality occurring in less complex habitats (Tupper and Boutilier 1995b). Fish that make use of less complex habitats, as a result of competition for space, will have a higher risk of mortality (Hunte and Cote 1989, Tupper and Boutilier 1995b). Habitat competition is one possible consequence that may cause variation in habitat use by sympatric species.

In addition to competition for habitat during years with high densities of juveniles, cannibalism is also likely to be high (Bjørnstad et al. 1999). In general, cannibalism is considered a density-dependent process (Garrison and Link 2000a) that increases with abundance (Anderson and Gregory 2000). For example, during years when adult cod and older juvenile populations are high, predation on younger juveniles should also be high (Anderson and Gregory 2000).

1.6 Background on Juvenile Gadid Research in Northeastern Newfoundland

In coastal Newfoundland, eelgrass (*Zostera marina*) has a special importance, as it plays a nursery role for young of the year gadids that settle in these habitats (Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003a). Every summer, juvenile white hake (*Urophycis tenuis*), Greenland cod (*G. ogac*), and Atlantic cod settle from the pelagic to a demersal juvenile lifestage in the nearshore areas of Newfoundland. Since 1995, seine surveys for fish have been taking place in Newman Sound, Terra Nova National Park, Newfoundland. Evidence from these surveys and other research on the northeast coast of Newfoundland have shown that the abundance of juvenile white hake in this area has been increasing, especially in the past few years (Laurel et al. submitted).

Component studies of this research have focused on timing and recruitment strength of first year gadids that settle in these coastal areas (eg. Laurel et al. 2003a, Ings 2005). Ings (2005), in particular, found that the recruitment of white hake and Greenland cod from the pelagic to the demersal juvenile lifestages in coastal areas on the northeast coast of Newfoundland have usually co-occurred during mid to late July. The smallest observed length at settlement to the demersal lifestage for juvenile white hake was 46 mm, while for Greenland cod it was 30 mm. In contrast, juvenile Atlantic cod settle in two to six recruitment pulses between August and November (Methven and Bajdik 1994, Grant and Brown 1998, Laurel et al. 2003a). The smallest observed length of Atlantic cod at settlement was 38-39 mm (Grant and Brown 1998, Ings 2005). All three of these Gadidae species prefer to settle in

eelgrass habitat as opposed to sand or mud substrates in coastal Newfoundland (Gregory and Laurel unpublished data).

1.7 Ecological Differences Among Three Juvenile Gadids

White hake are found in the Northwest Atlantic Ocean from Iceland to North Carolina (Musick 1974). Currently, little is known about white hake during their juvenile life history stage, especially in Newfoundland (Kulka et al. 2004). Juveniles of this species remain pelagic until they reach a size of ca. 50 to 80 mm TL, at which time they become demersal (Musick 1974, Markle et al. 1982). Markle et al. (1982) observed that the youngest demersal white hake juveniles inhabit coastal estuaries and shallow water, where their optimal temperature range seems to be 4-12°C. In particular, juvenile white hake show some preference for eelgrass habitats in these shallow, nearshore areas (Bigelow and Schroeder 1953, Fahay and Able 1989, Heck et al. 1989, Laurel et al. submitted).

Juvenile white hake have a "get big quick" life history strategy (Markle et al. 1982), with rapid growth rates of approximately 1 mm/day from June to October on the northeast coast of the United States and Nova Scotia (Fahay and Able 1989, Lang et al. 1996). Growth rates are slightly slower in Newman Sound, Newfoundland, and in 2005 rates averaged 0.81 mm/day from the start of August to the end of October (Gregory, in prep.). These growth rates allow young of the year white hake to reach lengths between 25 and 35 cm by the start of their first winter (Markle et al. 1982, Able and Fahay 1998).

As juveniles, white hake feed predominantly on crustaceans (Bowman 1981), with an increasing selection for fish in the diet as size increases (Garrison and Link

2000b). Garrison and Link (2000b) found that by 21-40 cm long, white hake were feeding mainly on shrimp and small fish.

Greenland cod are distributed farther north than white hake. They range from Alaska to Greenland and south to Cape Breton, Nova Scotia (Scott and Scott 1988). In contrast to white hake and Atlantic cod, Greenland cod have demersal eggs and spawn in nearshore areas (Scott and Scott 1988). *G. ogac* is a slow growing, demersal fish that remains near the coast for the duration of its life (Mikhail and Welch 1989). In Newman Sound, Newfoundland reported growth rates of first-year Greenland cod during 2005 averaged 0.67 mm/day from the start of August to the end of October (Gregory, in prep.).

Sheppard (2005) found that the maximum distance traveled by juvenile Greenland cod after settlement was only 400 m or less, suggesting that juveniles are site-specific. During their second year, age 1+ Greenland cod do not migrate or school, and show strong site-attachment (Mikhail and Welch 1989, Morin et al. 1991, Nielsen and Andersen 2001). In a field experiment in Newman Sound, Newfoundland, Laurel et al. (2003a) found that juvenile Greenland cod prefer to settle in eelgrass habitat. Results of this study also suggested that juvenile Greenland cod are more dependent on eelgrass for refuge than Atlantic cod.

Atlantic cod occurs on both sides of the North Atlantic. In the western North Atlantic their distribution ranges from Greenland and southern Baffin Island south to North Carolina (Scott and Scott 1988). For centuries Atlantic cod has been fished on the continental shelves of the North Atlantic (Scott and Scott 1988). However, in the early 1990's the northern cod stock from northern Labrador to the Grand Banks

collapsed (Taggart et al. 1994) and as a result it has been reduced to less than 1 % of its historical biomass (COSEWIC 2003, Lilly et al. 2004). The collapse of this stock prompted research on young Atlantic cod in Newfoundland and one consistent finding was the importance of nearshore areas as nursery habitat for juveniles (Keats and Steele 1992, Gotceitas et al. 1997, Anderson and Gregory 2000, Grant 2000, Linehan et al. 2001, Laurel et al. 2003a,b, Laurel et al. 2004, Ings et al. submitted). In particular, juvenile Atlantic cod use structurally complex habitats, specifically eelgrass (Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003a,b) and cobble (Gotceitas and Brown 1993, Gotceitas et al. 1995, Tupper and Boutilier 1995a, Fraser et al. 1996) as refuges to reduce predation risk.

Juvenile white hake grow more rapidly and recruit earlier to coastal Newfoundland than Greenland and Atlantic cod. These two factors allow hake to outgrow predation risk to some predators, while minimizing the time spent in the more vulnerable, smaller size classes. This size advantage may also lead to the competitive exclusion of other juvenile gadid species from optimal habitat during years when high densities of fish settle to nearshore areas. Optimal habitat is that which maximizes an organism's fitness within existing tradeoffs and constraints, and might be considered a composite of foraging opportunities (energy gain) versus predation risk (probability of death).

Because juvenile white hake have become more numerically abundant, especially over the past few years on the northeast coast of Newfoundland, it is pertinent that we learn about their habitat use and interactions with other gadids in these areas. Knowledge of habitat use and nursery requirements of juvenile fish are

key considerations for successful management of fish populations (Langton et al. 1996, COSEWIC 2003, Cote et al. 2004). Juvenile Greenland cod may well be the gadid species most strongly affected by interspecific interactions with juvenile white hake because of the Greenland cod's high affinity for eelgrass habitat and degree of temporal and spatial overlap with white hake in coastal Newfoundland. The objectives of this study are, therefore, to investigate the use of habitat and anti-predator behaviour of juvenile white hake and Greenland cod in response to predator threat and interspecific competition.

It was predicted there would be a high level of competition for refuge space between juvenile white hake and Greenland cod because of their use of similar habitat. In particular, I predicted that exposure to a predator threat when these two species overlap spatially and temporally will lead to habitat segregation of white hake and Greenland cod. More specifically, I predicted that white hake should occupy the safest, most complex habitats during interspecific situations, largely due to the size advantage that they obtain over Greenland cod shortly after settlement to the demersal lifestage.

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CO-AUTHORSHIP STATEMENT

Chapter 2: Predator-mediated habitat use by juvenile white hake (*Urophycis tenuis*) and Greenland cod (*Gadus ogac*)

Chris W. Lewis designed the research proposal, collected and organized all data, performed the statistical analysis and prepared the manuscript. Robert S. Gregory and Ian A. Fleming contributed with ideas and methods, and analysis and interpretation of the data. In addition, Robert S. Gregory and Ian A. Fleming reviewed the manuscript and suggested revisions.

CHAPTER 2

Predator-mediated habitat use by juvenile white hake (*Urophycis tenuis*) and Greenland cod (*Gadus ogac*)

2.1 Introduction

Predation is often a main cause of natural mortality during the early life stages of fish (Crowder 1980, Hunter 1981, Lima and Dill 1990, Sogard 1997), having dramatic affects on prey population dynamics, distribution, and ecosystems (Sih 1987, Lima 1998). Predation risk is one of the driving forces behind habitat selection by prey (reviewed by Lima and Dill 1990). Habitat selection is defined as the behavioural responses and environmental surroundings that lead to preference of one habitat over another (Meadows and Campbell 1972). In aquatic systems, vegetated habitats have been shown to act as important refuges (Orth et al. 1984, Keats et al. 1987, Gotceitas and Colgan 1989, Gotceitas et al. 1997, Rangeley and Kramer 1998, Linehan et al. 2001, Heck et al. 2003, Laurel et al. 2003a) due to the decreased foraging efficiency of piscivorous predators within them (Savino and Stein 1982, Persson and Eklov 1995). Specifically, seagrass habitats are thought to play such a role in marine ecosystems (Orth et al. 1984, Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003a).

At high densities of juvenile fish, refuge habitats can potentially reach carrying capacity and become a limiting resource (Johnson et al. 1988, Laurel et al. 2004, Blanchard et al. 2005). The "resource-limitation" theory suggests that such factors may in turn regulate fish populations (Hunte and Cote 1989). Competition intensifies as prey are forced into a common refuge (Sih 1987) and habitat exclusion

is one possible outcome. This may cause differences in habitat use by sympatric species.

In the nearshore, coastal waters of Newfoundland, age-0 Greenland cod (*Gadus ogac*) and Atlantic cod (*G. morhua*) co-habit as demersal juveniles from August to late December (Methven and Bajdik 1994, Gotceitas et al. 1997, Grant and Brown 1998a, Methven et al. 2001, Laurel et al. 2003a). Greenland cod recruit to coastal areas in a single pulse during early August (Laurel et al. 2003a), at approximately the same time as the recruitment of white hake (*Urophycis tenuis*) (Ings et al. submitted). During the demersal juvenile stage, these two gadid species together with the Atlantic cod frequent eelgrass (*Zostera marina*) habitat moreso than sand or mud habitats (Gregory and Laurel unpublished data).

Greenland cod are distributed from Alaska to Greenland and south to Cape Breton, Nova Scotia (Scott and Scott 1988). *G. ogac* is slow growing (Mikhail and Welch 1989), and in 2005, growth rates averaged 0.67 mm/day for first-year fish from the start of August to the end of October in Newman Sound, Newfoundland (Gregory, in prep.). Greenland cod are demersal and remain near the coast for the duration of their life (Mikhail and Welch 1989). Sheppard (2005) found that the maximum distance traveled by juvenile Greenland cod after settlement was 400 m, providing evidence that juveniles of this species are site-specific. During their second year, age 1+ Greenland cod do not migrate or school and continue to show strong site-attachment (Mikhail and Welch 1989, Morin et al. 1991, Nielsen and Andersen 2001). Field experiments in Newman Sound, Newfoundland have found that juvenile Greenland cod settle in eelgrass habitat (Laurel et al. 2003a, Thistle 2006).

White hake are distributed in the northwest Atlantic Ocean from Iceland and southern Labrador south to North Carolina (Musick 1974). At present, there is little known about the behaviour of juvenile white hake, especially in Newfoundland (Kulka et al. 2004). In waters south of Newfoundland, demersal juvenile hake are found in warm (Musick 1973), shallow, nearshore waters (Markle et al. 1982, Fahay and Able 1989, Heck et al. 1989), where they associate with eelgrass (Bigelow and Schroeder 1953, Fahay and Able 1989, Heck et al. 1989). Juvenile white hake have a fast growing life history strategy (Markle et al. 1982), with rapid growth rates of approximately 1 mm/day from June to October on the northeast coast of the United States and Nova Scotia (Fahay and Able 1989, Lang et al. 1996). Growth rates are slightly slower in Newman Sound, Newfoundland, and in 2005 only averaged 0.81 mm/day from the start of August to the end of October (Gregory, in prep.). High growth rates allow young of the year white hake to reach lengths between 25 and 35 cm by the start of their first winter (Markle et al. 1982, Able and Fahay 1998). This size advantage could have negative impacts on other co-habiting juvenile gadids if they grow more slowly, and/or settle later. Negative impacts could directly and/or indirectly (i.e. displacement from preferred habitat) increase predation risk.

There has been an increase in juvenile white hake abundance on the northeast coast of Newfoundland indicative of a northward expansion of their distribution (Laurel et al. submitted). Through the past decade, the density of juveniles of Atlantic cod in coastal nurseries has been negatively correlated with white hake density (Laurel et al. submitted). The northern distribution expansion and increasing abundance of white hake could thus be affecting the habitat use and behaviour of

other juvenile fish that settle in coastal Newfoundland. The two species most likely to be affected by this increase in hake density are juvenile Atlantic cod and Greenland cod, both of which appear to show strong affinity for eelgrass habitat, and overlap with white hake spatially and temporally (Thistle 2006). Since Greenland cod has the strongest eelgrass affinity of the two cod species (Laurel et al. 2003a, Thistle 2006) and the greatest degree of temporal overlap, it is most likely to be affected by white hake.

In my study, I investigated the use of habitat and behaviours of juvenile white hake and Greenland cod in response to predatory threat and interspecific competition in a laboratory setting. Because juvenile white hake and Greenland cod use similar habitat and settle to nearshore Newfoundland at approximately the same time, I predicted the potential for habitat competition to be high. In addition, I predicted that during interspecific situations when exposed to a predator, the size advantage seen in first year white hake will allow them to displace Greenland cod from their preferred habitats.

2.2 Materials and Methods

2.2.1 Study Species

Juvenile Greenland cod (*Gadus ogac*) were collected by beach seine from Newman Sound, Terra Nova National Park, Newfoundland in August 2005 and juvenile white hake (*Urophycis tenuis*) from St. Mary's Bay, Newfoundland in September 2005 (Figure 2.1). All juvenile fish were transported in aerated tanks from the field to the Ocean Sciences Centre in Logy Bay, Newfoundland. At the Ocean

Sciences Centre, each species were held in separate flow-through holding tanks (1.0 x 1.0 x 0.5 m for cod and 2.0 x 2.0 x 0.5 m for hake) and fed chopped herring (*Clupea harengus*) daily to satiation.

Age 3+ Atlantic cod (*Gadus morhua*, 47.5 ± 0.5 cm, 1 SE) were collected by hand line in November 2005 from Logy Bay, Newfoundland (Figure 2.1) for use as predators in this study. Age 3+ Atlantic cod have been used successfully in previous laboratory experiments to elicit behavioural responses from juvenile gadids (Gotceitas and Brown 1993, Gotceitas et al. 1995, Fraser et al. 1996, Gotceitas et al. 1997). Older Atlantic cod (age 1+, 2+, and 3+) are also known to spatially overlap with juvenile gadids in coastal Newfoundland (Linehan et al. 2001, Laurel et al. 2003b). The predator-juvenile length ratio ranged from 1.9-4.9:1 at the time of experimentation. Atlantic cod were held in a flow-through holding tank (3.0 m diameter x 1.5 m depth) at the Ocean Sciences Centre and fed chopped herring once every four days. This resulted in the fish being fed two days prior to use, causing predators to be hungry, but not starving during experiments.

All holding tanks were supplied with seawater that was maintained between 5 and 10°C. Photoperiod was controlled using timers to mimic the natural diel/nocturnal cycles for the latitude and season.

2.2.2 Experimental Setup

Two flow-through tanks (2.0 x 2.0 x 0.5 m), surrounded by a blind in a lab isolated from disturbance were used as test arenas. The water depth (0.5 m) of these experimental tanks was common to all species and has been successfully used in other laboratory experiments that monitored habitat use of juvenile Atlantic cod (eg.

Gotceitas and Brown 1993, Gotceitas et al. 1995, Fraser et al. 1996, Gotceitas et al. 1997). The bottoms of each of these tanks were divided into thirds of 1.3 m^2 each and covered with artificial eelgrass, cobble, or sand (Figure 2.2). Artificial eelgrass habitat was constructed from green polypropylene ribbon (W: 0.5 cm, H: 20 cm) attached to a wire mesh base at a density of 400 blades/m^2 and covered with sand to a depth of 10 cm. The 400 blades/m^2 was selected to be well within the natural range of eelgrass blade density (Orth et al. 1984). Cobble consisted of beach stone (5 – 12 cm in diameter), whereas sand habitat consisted of fine-grained substrate (< 0.1 cm in diameter). Cobble and sand covered the bottom of each tank to a depth of 10 cm (substrate setup adapted from Gotceitas et al. 1995, Gotceitas et al. 1997, Laurel et al. 2004). Mineral substrates were representative of the coastal environment ($\leq$ 25 m in depth) in Newfoundland (Gotceitas et al. 1995). Water flows in each of the tanks were controlled by connecting water tubing between the standpipe and each of the substrate boundaries and adjusting accordingly. This lab based experiment provided a setting to observe habitat use and behaviours in a common controlled environment, which cannot easily be done in the natural environment.

Two "predator chambers" (1.0 x 1.0 x 0.5 m) were constructed out of black coroplast (a rigid plastic). One chamber was used in each of the experimental arenas in order to house the predator for the evening prior to release. Pulley systems were used to raise and lower the "predator chambers" from behind the observation blind to release each predator into an arena.

Both experimental tanks were supplied with seawater that was maintained between 5 and 10°C, to match temperatures in the holding tanks. Sunrise and sunset

times for each experimental trial were controlled by natural light shining in through windows from an adjacent room. Light intensities were increased prior to and decreased after observations each day.

Primary habitat choice and behaviours of both juvenile white hake and Greenland cod were first assessed in intraspecific situations. In these situations, eight groups of four juveniles of each species were observed before and during predator exposure. After intraspecific behaviours were observed, interspecific behaviours were assessed before and during predator exposure using eight groups of two juvenile white hake and two Greenland cod together. Interspecific situations allowed for habitat use and behaviours to be monitored in low (no predator) and high risk conditions (predator present). Experimental densities of juvenile white hake and Greenland cod were consistent with densities observed in Newman Sound, Terra Nova National Park, Newfoundland. Specifically, juvenile white hake and Greenland cod natural densities have been reported as high as $0.5/m^2$ and $1.5/m^2$, respectively (Gregory, in prep.).

2.2.3 Experimental Design: Intraspecific Competition

Groups of either four juvenile white hake (Range: 151-244 mm; Mean ± 1 SE: 191.28 ± 3.58 mm) or four juvenile Greenland cod (Range: 95-142 mm; Mean ± 1 SE: 125.59 ± 1.95 mm) were used for each set of experimental trials. Feeding was terminated on the day before introduction to the experimental tank. All fish were naïve to the experiments (i.e. none were used more than once). The day prior to the start of observations, fish were lightly anaesthetized to a state of equilibrium loss and reduced operculum movement using 2-phenoxyethanol (0.25 ml/L). The fish were

then tagged with two colored beads (2 mm diameter) that were attached with surgical thread to the dorsal musculature, anterior to the dorsal fin. The tagging of fish allowed for differentiation between individuals during the course of the experiment. After tagging, the four juvenile white hake were released into one experimental arena and the four Greenland cod were released into the other. All fish were allotted a minimum of 20 hours to recover and acclimatize to the experimental conditions after the tagging procedure.

Each trial lasted two days, with the fish being tested in the absence of a predator during day 1 and in the presence of a predator during day 2. The same methods were used for fish in both of the experimental arenas, however, there was about a 15 minute difference in the timing of events and observations between the two. At 08:45 on the morning of the first day of the trial, the tank flow was shut off in one of the experimental arenas, and at 09:05 the predator chamber was raised. At 09:10 the experimental trial commenced and each of the four juvenile fish were observed for six two-minute observation periods during each treatment. Sampling times took place at 09:10, 10:30, 11:50, 13:10, 14:30, and 15:50. Juvenile fish habitat use and behaviours (Table 2.1) were recorded using a PSION observation recorder (Noldus Information Technology, Wageningen, The Netherlands). After the final sampling time on each day, water flow was turned on again and the predator chamber was lowered back into the tank. The predator chamber was raised and lowered, prior to and after observations each day, respectively, in order to keep experimental conditions as consistent as possible.

At the end of the first day of observations, an age 3+ Atlantic cod was introduced to each predator holding chamber. Two predators were selected from the holding tank to be used for the predator exposure treatments. On the morning of the second day of observations, the predators were released from each chamber using pulley systems. Juvenile fish observations started immediately after each predator was released. Predator habitat use and behaviours were also recorded at each of the six sampling times, as in the previous day. At the end of the second day of observations, the predators were removed from each of the experimental tanks and returned to their holding tanks. During every successive replicate the two predators were rotated between juvenile species for use in the predator exposure treatment, meaning that during the course of this experiment four groups of juveniles from each species were exposed to one age 3+ Atlantic cod predator, while the other four groups of juveniles were exposed to the other age 3+ Atlantic cod predator.

After four complete sets of observations on each species, the habitat locations in each experimental tank were rotated, meaning at least two of the substrates positions were swapped. In total, eight groups of four juveniles of each species were observed. All observations were made during the day because predation risk is highest at this time (Linehan et al. 2001). Furthermore, it has been suggested that first-year Atlantic and Greenland cod are primarily daytime feeders (Grant and Brown 1998b, Thistle 2006, M. Thistle pers. comm.), whereas first-year white hake are pre-dominantly night time feeders (Methven et al. 2001).

2.2.4 Experimental Design: Interspecific Competition

Combined groups of two juvenile white hake (Range: 194-257 mm; Mean ± 1 SE: 216.63 ± 3.58 mm) and two juvenile Greenland cod (Range: 136-171 mm; Mean ± 1 SE: 149.56 ± 2.48 mm) were used to assess interspecific habitat use and behaviours. All fish in the interspecific trials had been used in the intraspecific trials and were therefore, similarly experienced to the test conditions. Tags from the intraspecific competition experiments had remained in place and new tags were not necessary. Fish were lightly anaesthetized using 2-phenoxyethanol (0.25 ml/L of water) to be consistent with the previous pre-experimental conditions. After anaesthetization, one group of four juvenile fish was released into one experimental arena, while the other group was released into the other arena. Post-anesthetic, fish were allotted a minimum of 20 hours to recover and acclimate to the experimental environment.

The observation routine followed that described for the intraspecific competition experiments.

After four complete sets of trials, the habitat locations in each experimental tank were rotated, meaning at least two of the substrates positions were swapped. In total, eight groups of four juveniles were observed in interspecific situations.

2.2.5 Data Analysis

All statistical analyses were performed using Systat version 9. Model residuals from statistical tests were assessed for normality, randomness, independence, additivity, and homogeneity of variance (Sokal and Rohlf 1995) to determine whether any assumptions of ANOVA were violated.

To determine if there was any habitat preference by juvenile white hake or Greenland cod in the absence of a predator and interspecific competitor t-tests were used.

For analysis of habitat use and behaviours of fish in intraspecific situations, 2-way ANOVAs were initially performed using the General Linear Model (GLM) within the factors of time (09:10, 10:30, 11:50, 13:10, 14:30, and 15:50) and predator treatment. For analysis of habitat use and behaviours of fish in interspecific situations, 3-way ANOVAs were initially performed using the GLM within the factors of time (09:10, 10:30, 11:50, 13:10, 14:30, and 15:50), juvenile species, and predator treatment.

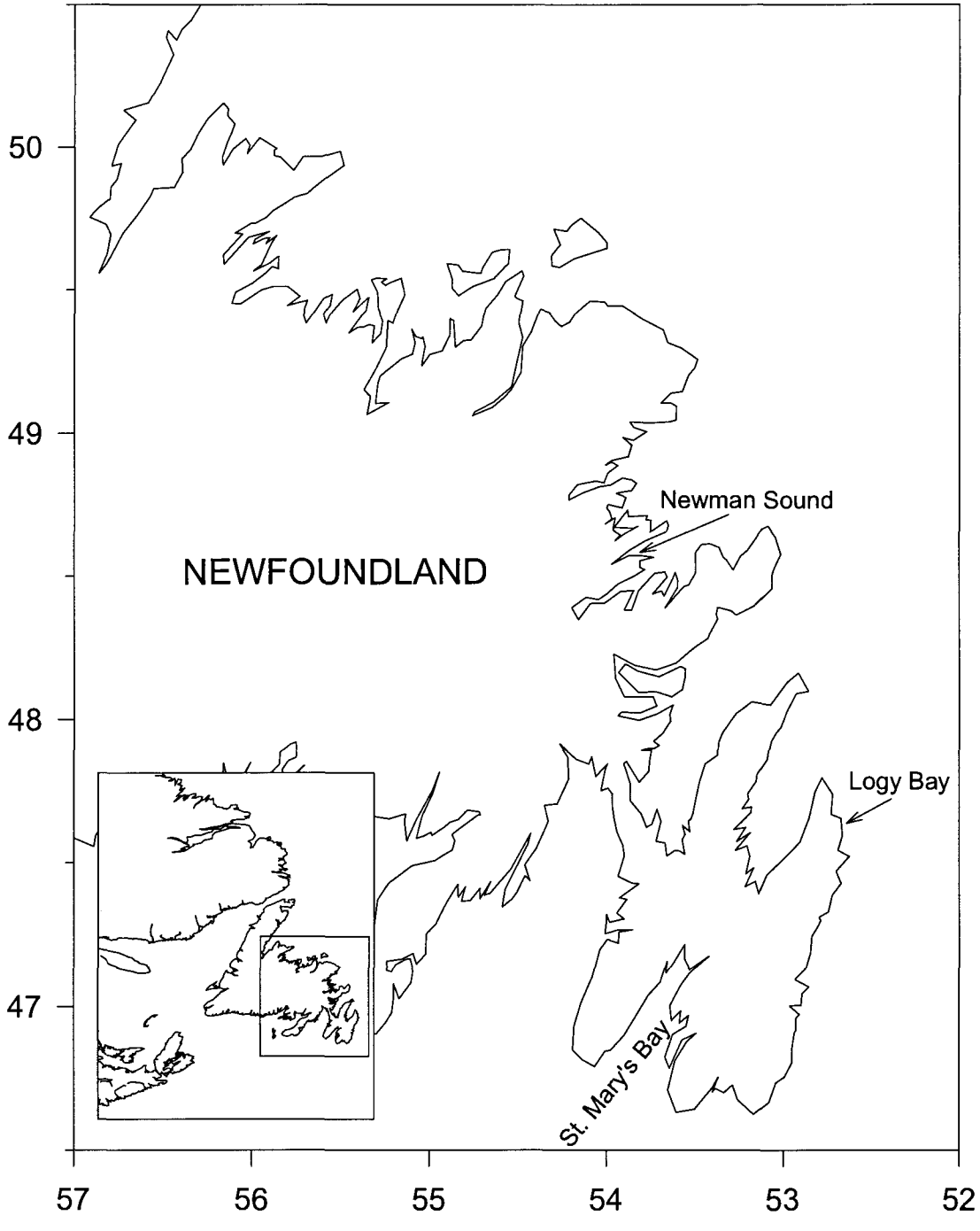

Figure 2.1. Collection sites for juvenile white hake (St. Mary's Bay), juvenile Greenland cod (Newman Sound), and age 3+ Atlantic cod (Logy Bay) in coastal Newfoundland, Canada (from D. Ings).

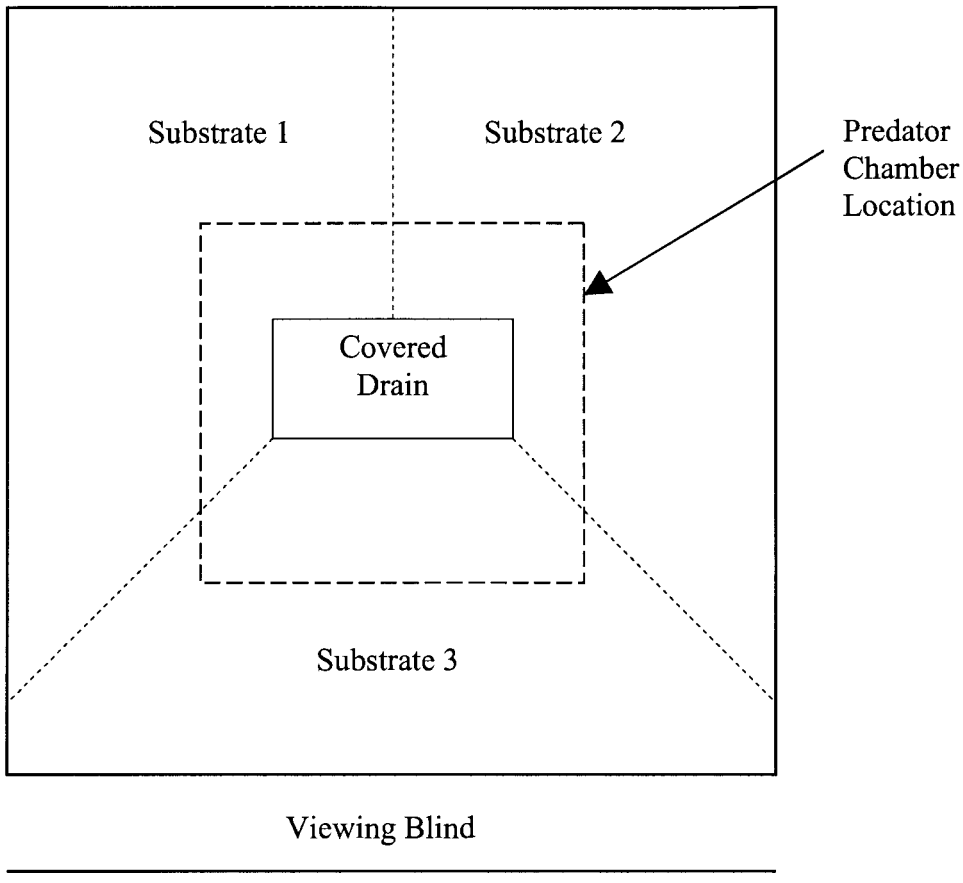

Figure 2.2. Top view of experimental tank (2 x 2 x 0.5 m) setup showing substrate distribution pattern and predator chamber location.

Table 2.1. Description of behaviours observed for juvenile fish.

Behaviour	Description
Concealed	within a cobble crevice or below the top of eelgrass blades
In Open	above sand, cobble, or the top of eelgrass blades
Moving	swimming
Motionless	no movement or swimming; staying in one place
Chasing	follows another fish; usually results in other fish fleeing
Fleeing	quickly swims away from an approaching or chasing fish

Note: Concealed-In Open behaviours are mutually exclusive.
Moving-Motionless behaviours are mutually exclusive.

2.3 Results

2.3.1 Habitat Use

Habitat use by juvenile white hake and Greenland cod in the absence of a predator and interspecific competitor was similar in the ordering of preference (Figure 2.3). The expected average time for an individual to spend in or above artificial eelgrass, cobble, or sand was a third of the observation time or 40 seconds. Specifically, the results showed that both species used cobble habitat no more or less than expected (t-test: white hake: $t = -0.87$, $p = 0.389$; Greenland cod: $t = -0.63$, $p = 0.533$), however, they both used sand habitat significantly less than expected (t-test: white hake: $t = -4.75$, $p < 0.001$; Greenland cod: $t = -3.21$, $p = 0.003$). In addition, Greenland cod used artificial eelgrass significantly more than expected (t-test: $t = 2.80$, $p = 0.009$), while white hake used artificial eelgrass no more or less than expected (t-test: $t = 1.42$, $p = 0.165$).

2.3.2 Predator Effects on Juvenile White Hake

There was no significant difference in activity levels of the two predators ($F_{1,6} = 0.993$, $p = 0.357$; Figure 2.4). Additionally, there was no difference in the number of times that the predators swam over any of the habitat substrates ($\chi^2 = 0.176$; $df = 2$, $p > 0.05$). Based on these findings, it was assumed that both predators influenced habitat use and behaviour of juvenile white hake similarly. Therefore, the two predators were not delineated in subsequent analyses.

The time spent by juvenile white hake in or over artificial eelgrass, cobble, and sand, as well as time spent concealed and motionless were compared for six time periods (9:10, 10:30, 11:50, 13:10, 14:30, and 15:50) between two variables: no

predator (control) and exposure to a predator. Results from general linear models found no significant interaction between time and predator treatment for any of the dependent variables (Table 2.2). There were also no statistically significant differences in time spent using artificial eelgrass, cobble, sand, or in the time spent concealed and motionless (Table 2.2) during the different times of day. Because time period had no significant effect on the variables examined; the model was simplified from a two-way to a one-way ANOVA by dropping time period as an explanatory variable. The effects of predator presence (age 3+ Atlantic cod) were then assessed by comparing the average time in or above each habitat and the behaviours of each individual fish among predator treatments.

The reduced models indicated no statistically significant differences in the time spent by hake in or above artificial eelgrass, cobble, or sand before or during predator exposure (Table 2.3; Figure 2.5). There was also no significant difference in the time spent concealed and motionless before or during exposure to a predator (Table 2.3; Figure 2.5).

2.3.3 Predator Effects on Juvenile Greenland Cod

Similar to the trials with white hake, a general linear model indicated no significant difference in the activity levels of the predators ($F_{1,6} = 0.219$, $p = 0.657$; Figure 2.4) during the Greenland cod trials. Therefore, the predators were not delineated in subsequent analyses. However, there was a consistent pattern in habitat use by the predators ($\chi^2 = 7.650$; $df = 2$, $p < 0.05$). The predators spent more time over the artificial eelgrass substrate than the cobble substrate.

The time spent in or over artificial eelgrass, cobble, and sand, as well as time spent concealed and motionless by juvenile Greenland cod was compared for six time periods among two variables: no predator (control) and exposure to a predator. Results from general linear models found no significant interaction between time and predator treatment for any of the dependent variables (Table 2.4). For time period (9:10, 10:30, 11:50, 13:10, 14:30, and 15:50), there were no statistically significant differences found in time spent using artificial eelgrass, cobble, sand, or the time spent concealed (Table 2.4; Figure 2.6). However, the time spent motionless changed with time period and decreased during predator exposure (Table 2.4; Figure 2.6). Because time period had no significant effect on the variables examined, except for the motionless behaviour, the model was simplified from a two-way to a one-way ANOVA for all other variables by dropping time period as an explanatory variable. The effects of predator presence (age 3+ Atlantic cod) were then assessed by comparing the average time in or above each habitat and the time spent concealed for each individual fish among predator treatments.

There were no statistically significant differences in time spent in or above artificial eelgrass, cobble, or sand in the presence versus absence of a predator (age 3+ Atlantic cod; Table 2.5; Figure 2.6). Furthermore, there was no significant change in the time spent concealed during predator exposure (Table 2.5; Figure 2.6).

2.3.4 Predator Effects on Interspecific Competition

A general linear model revealed a significant difference in activity levels (time spent swimming) of the two predators used during the interspecific experiment ($F_{1,6} = 291.241$, $p < 0.001$). Based on the significantly lower activity levels of

Predator # 1 compared to Predator # 2 (Figure 2.4), juvenile habitat use and behaviours were analyzed separately for each predator. Predator # 1 will henceforth be referred to as the "passive" predator because of its lower levels of swimming activity and Predator # 2 as the "active" predator. Additonally, there were no consistent patterns of habitat use by Predators # 1 ($\chi^2 = 1.300$; df = 2, $p > 0.05$) or # 2 ($\chi^2 = 2.086$; df = 2, $p > 0.05$).

2.3.4.1 Passive Predator Effects

A general linear model was used to statistically compare the time spent using eelgrass, cobble, and sand, as well as time spent concealed and motionless in terms of time of day (09:10, 10:30, 11:50, 13:10, 14:30, and 15:50), juvenile species (white hake or Greenland cod), and predator treatment condition (presence or absence of the passive age 3+ Atlantic cod). Results from general linear models found no significant interaction among time, juvenile species and predator treatment, between time and predator treatment, or between time and juvenile species for any of the dependent variables ($p > 0.05$). Results from the models also indicated time period had no significant effect on time spent in or above artificial eelgrass, cobble, sand, or time spent concealed and motionless ($p > 0.05$). Because time period had no significant effect on the variables examined; the model was simplified from a three-way to a two-way ANOVA by dropping time period as an explanatory variable. Observations made at different time periods were collapsed for each individual fish and the average time per habitat and behaviour was used as a means to compare differences among the other two explanatory behaviours, juvenile species and predator treatment condition.

Results from the general linear models found no significant interaction between predator treatment and juvenile species for each of the dependent variables examined (Table 2.6). However, there was a significant decrease in the time spent in or above artificial eelgrass, no significant difference in time spent in or above cobble or sand during exposure relative to pre-exposure to the "passive" predator (Table 2.6; Figure 2.7). In addition, there were significant decreases in the time spent concealed and motionless during exposure relative to pre-exposure to the "passive" predator (Table 2.6; Figure 2.7). There was no significant difference in the time spent in or above artificial eelgrass between juveniles of the two species, but juvenile white hake spent more time in or above cobble and less time above sand than Greenland cod (Table 2.6; Figure 2.7). In addition, juvenile white hake spent significantly more time concealed and motionless than Greenland cod (Table 2.6; Figure 2.7).

2.3.4.2 Active Predator Effects

Results from general linear models found no significant interaction among time, juvenile species, and predator treatment, between time and predator treatment, or between time and juvenile species for any of the dependent variables ($p > 0.05$). In addition, time period had no significant effect on time spent in or above artificial eelgrass, cobble, sand, or time spent concealed and motionless ($p > 0.05$). Because time period had no significant effect on the variables examined; the model was simplified from a three-way to a two-way ANOVA by dropping time period as an explanatory variable. Observations made at different time periods were collapsed for each individual fish and the average time per habitat and behaviour was used as a

means to compare differences among the other two explanatory behaviours, juvenile species and predator treatment condition.

Results from the general linear models found no significant interaction between predator treatment and juvenile species for each of the dependent variables examined (Table 2.7). Similar to the "passive" predator, the presence of the "active" predator relative to no predator did not affect time spent in or above artificial eelgrass, cobble, or sand (Table 2.7; Figure 2.8). Moreover, time spent concealed and motionless remained constant before relative to during exposure to the "active" predator (Table 2.7; Figure 2.8). Hake juveniles spent significantly more time in artificial eelgrass, less time above sand, and did not differ in time spent in or above cobble compared to Greenland cod (Table 2.7; Figure 2.8). Furthermore, while juvenile white hake did not differ in the amount of time concealed, they did spend significantly more time motionless than Greenland cod (Table 2.7; Figure 2.8).

2.3.5 Agonistic Behaviour Observations

During the interspecific experiment, juvenile white hake chased other juvenile white hake and Greenland cod a total of 14 times and fled from other juvenile white hake, as well as predators 48 times in 384 minutes of observations. In contrast, in a total of 384 minutes of observations, juvenile Greenland cod did not exhibit any chasing behaviour and fled from other juveniles, as well as predators 58 times.

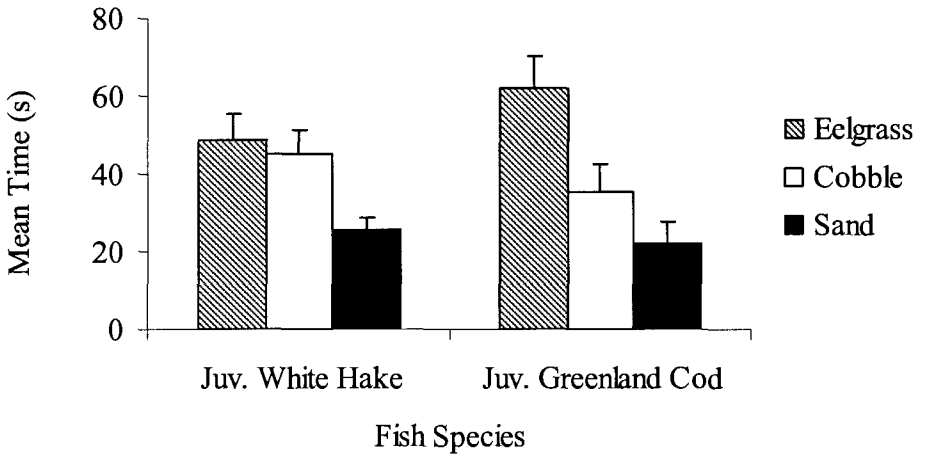

Figure 2.3. Mean time (s ± 1 SE; n = 32 for each bar) per observation spent using eelgrass, cobble, and sand substrates by juvenile white hake and Greenland cod during intraspecific situations.

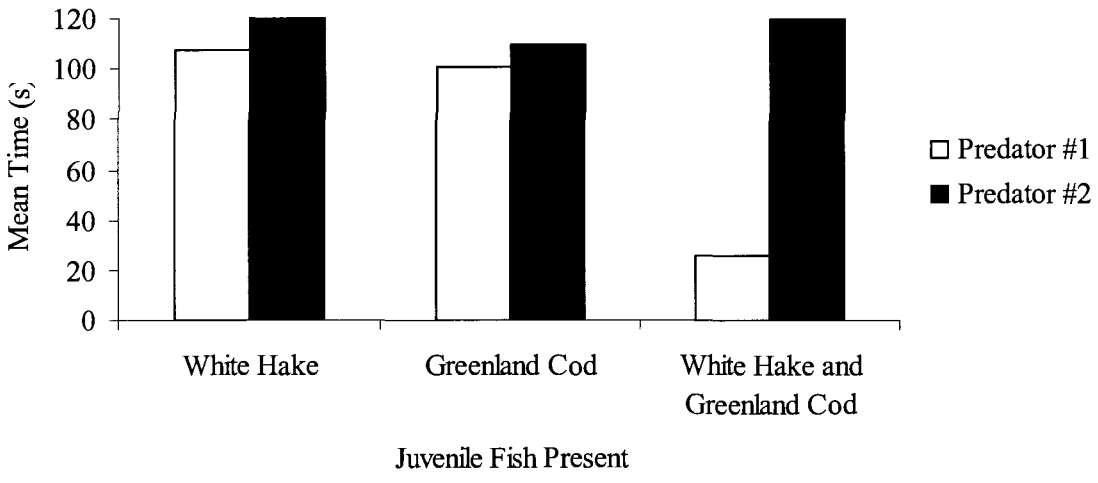

Figure 2.4. Mean time (s ± 1 SE) spent moving by Predator # 1 and # 2 in the intra- and interspecific competition experiments.

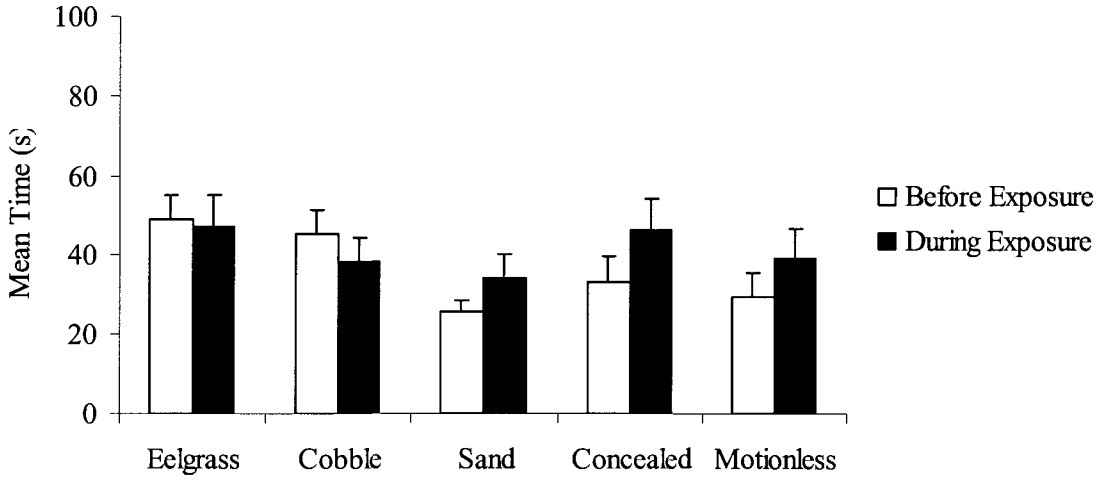

Figure 2.5. Mean time (s ± 1 SE; n = 32 for each bar) spent using eelgrass, cobble, or sand, and time spent concealed and motionless by juvenile white hake before and during exposure to a predator in the intraspecific competition experiment.

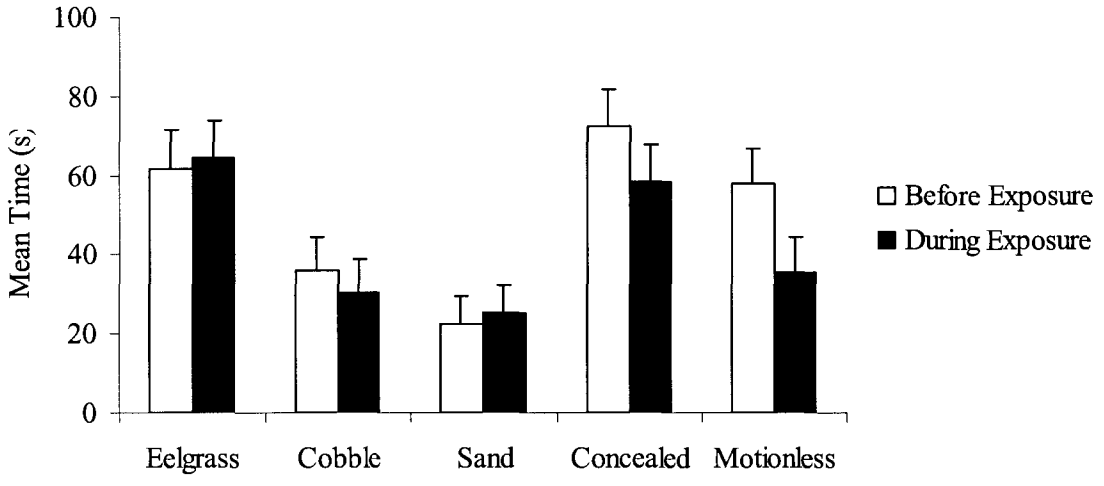

Figure 2.6. Mean time (s ± 1 SE; n = 32 for each bar) spent using eelgrass, cobble, or sand, as well as time spent concealed and motionless by juvenile Greenland cod before and during exposure to a predator in the intraspecific competition experiment.

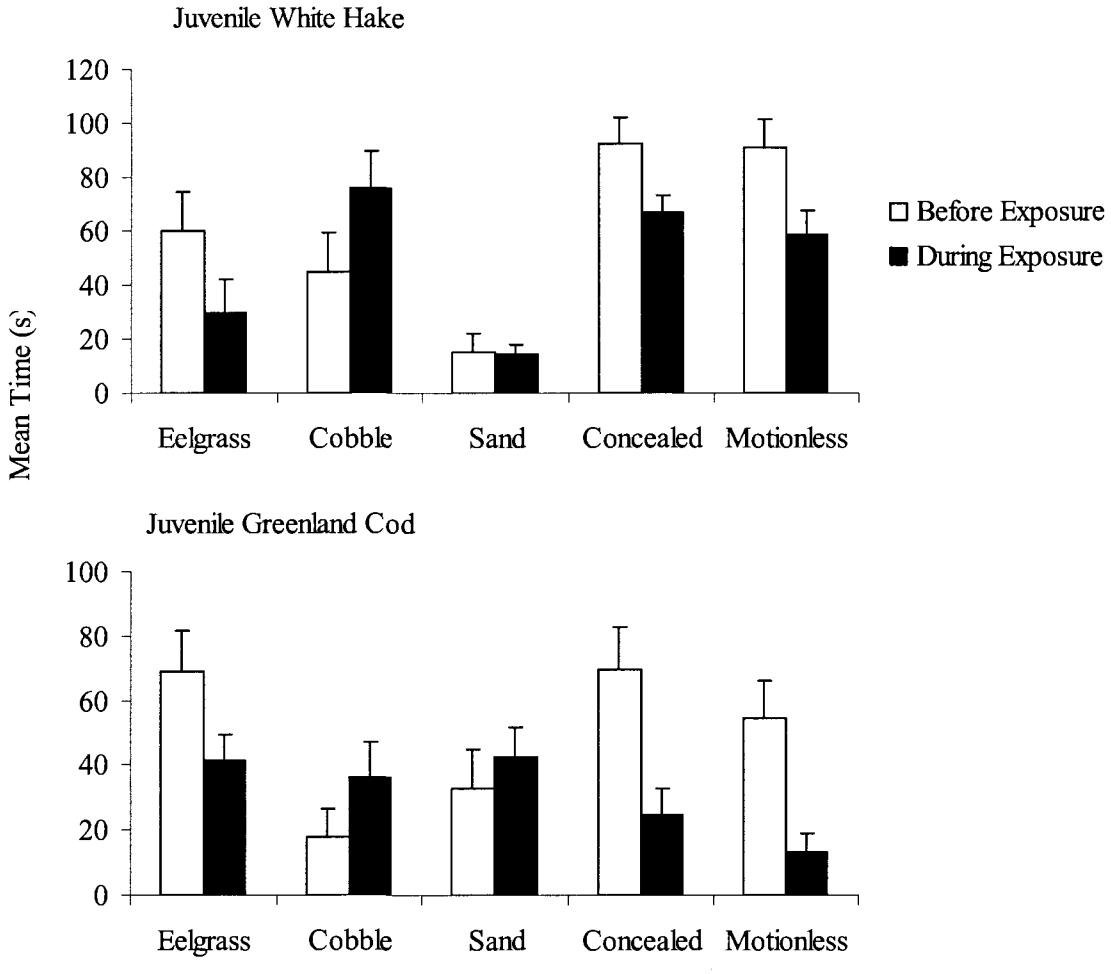

Figure 2.7. Mean time (s ± 1 SE n = 16 for each bar) spent using eelgrass, cobble, or sand, and time spent concealed and motionless by juvenile white hake and Greenland cod before and during exposure to a passive predator in the interspecific competition experiment.

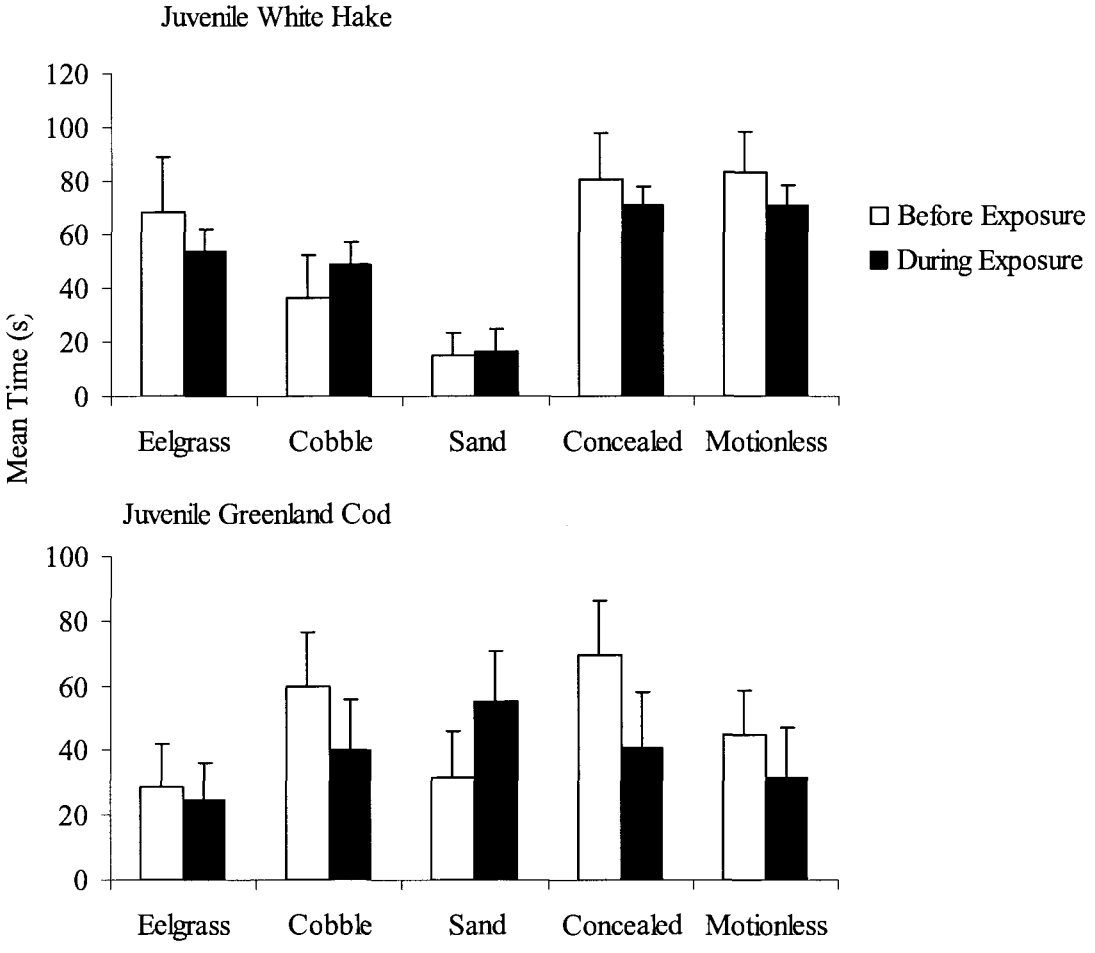

Figure 2.8. Mean time (s ± 1 SE; n = 16 for each bar) spent using eelgrass, cobble, or sand, and time spent concealed and motionless by juvenile white hake and Greenland cod before and during exposure to an active predator in the interspecific competition experiment.

Table 2.2. Results of two-way ANOVA analysis on factors influencing juvenile white hake behaviour (intraspecific).
* indicates a significant difference ($p < 0.05$).

Dependent Variable	Source	df	F-ratio	p
Concealed	Treatment	1	5.883	0.016*
	Time	5	0.870	0.501
	Treatment x Time	5	1.598	0.160
Motionless	Treatment	1	3.947	0.048*
	Time	5	0.588	0.709
	Treatment x Time	5	0.842	0.521
In or Above Eelgrass	Treatment	1	0.236	0.627
	Time	5	1.055	0.385
	Treatment x Time	5	0.502	0.775
In or Above Cobble	Treatment	1	1.645	0.200
	Time	5	0.588	0.709
	Treatment x Time	5	0.216	0.956
Above Sand	Treatment	1	4.772	0.030*
	Time	5	1.427	0.214
	Treatment x Time	5	1.293	0.266

Table 2.3. Results of one-way ANOVA analysis on factors influencing juvenile white hake behaviour (intraspecific).

Dependent Variable	Source	df	F-ratio	p
Concealed	Treatment	1	1.623	0.207
Motionless	Treatment	1	1.136	0.291
In or Above Eelgrass	Treatment	1	0.028	0.867
In or Above Cobble	Treatment	1	0.641	0.427
Above Sand	Treatment	1	1.667	0.202

Table 2.4. Results of two-way ANOVA analysis on factors influencing juvenile Greenland cod behaviour (intraspecific). * indicates a significant difference ($p < 0.05$).

Dependent Variable	Source	df	F-ratio	p
Concealed	Treatment	1	6.654	0.010*
	Time	5	1.980	0.081
	Treatment x Time	5	0.869	0.502
Motionless	Treatment	1	19.492	< 0.001*
	Time	5	4.221	< 0.001*
	Treatment x Time	5	1.428	0.213
In or Above Eelgrass	Treatment	1	0.246	0.620
	Time	5	2.143	0.060
	Treatment x Time	5	0.843	0.520
In or Above Cobble	Treatment	1	1.258	0.263
	Time	5	1.629	0.151
	Treatment x Time	5	0.528	0.755
Above Sand	Treatment	1	0.419	0.518
	Time	5	1.081	0.370
	Treatment x Time	5	1.404	0.222

Table 2.5. Results of one-way ANOVA analysis on factors influencing juvenile Greenland cod behaviour (intraspecific).

Dependent Variable	Source	df	F-ratio	p
Concealed	Treatment	1	1.863	0.177
In or Above Eelgrass	Treatment	1	0.043	0.835
In or Above Cobble	Treatment	1	0.332	0.567
Above Sand	Treatment	1	0.152	0.698

Table 2.6. Results of two-way ANOVA analysis on factors influencing juvenile fish behaviour (interspecific - passive predator).
* indicates a significant difference ($p < 0.05$).

Dependent Variable	Source	df	F-ratio	p
Concealed	Species	1	11.318	0.002*
	Treatment	1	12.965	0.001*
	Treatment x Species	1	1.002	0.326
Motionless	Species	1	18.813	< 0.001*
	Treatment	1	15.569	< 0.001*
	Treatment x Species	1	0.213	0.648
In or Above Eelgrass	Species	1	0.728	0.401
	Treatment	1	5.602	0.025*
	Treatment x Species	1	0.007	0.934
In or Above Cobble	Species	1	7.293	0.012*
	Treatment	1	4.055	0.054
	Treatment x Species	1	0.258	0.616
Above Sand	Species	1	7.024	0.013*
	Treatment	1	0.245	0.624
	Treatment x Species	1	0.369	0.548

Table 2.7. Results of two-way ANOVA analysis on factors influencing juvenile fish behaviour (interspecific - active predator).
* indicates a significant difference ($p < 0.05$).

Dependent Variable	Source	df	F-ratio	p
Concealed	Species	1	1.331	0.258
	Treatment	1	1.154	0.291
	Treatment x Species	1	0.276	0.603
Motionless	Species	1	5.918	0.022*
	Treatment	1	0.620	0.438
	Treatment x Species	1	0.001	0.982
In or Above Eelgrass	Species	1	4.447	0.044*
	Treatment	1	0.319	0.576
	Treatment x Species	1	0.099	0.755
In or Above Cobble	Species	1	0.190	0.667
	Treatment	1	0.039	0.845
	Treatment x Species	1	0.908	0.349
Above Sand	Species	1	4.544	0.042*
	Treatment	1	0.976	0.332
	Treatment x Species	1	0.738	0.398

2.4 Discussion

My results demonstrated that in intraspecific situations when no predator was present, both juvenile white hake (*Urophycis tenuis*) and Greenland cod (*Gadus ogac*) selected complex habitats as primary bottom substrate over sand. These findings were consistent with field observations from coastal Newfoundland (Gregory and Laurel unpublished data), as well as other studies on juvenile white hake (Bigelow and Schroeder 1953, Fahay and Able 1989, Heck et al. 1989, Thistle 2006) and Greenland cod (Laurel et al. 2003a, Thistle 2006). Additionally, when hake and cod were exposed to a predator during an intraspecific setting, there were no significant changes in the time spent using eelgrass, cobble, or sand substrates. Both species continued to make greater use of the safer, more structurally, complex habitats.

These observations suggest that juvenile white hake and Greenland cod are cautious fish, and that during exposure to a predator they continue to use structurally complex habitats as a risk-reducing strategy. Specifically, complex habitats reduce the foraging abilities of piscivores (Savino and Stein 1982, Gotceitas and Colgan 1989, Matilla 1992, Persson and Eklov 1995) and result in less risk of predation for juvenile fish compared to those that use barren or open habitats (Savino and Stein 1982, Werner et al. 1983a,b, Orth et al. 1984, Mittelbach 1986, Gotceitas and Colgan 1989, Gotceitas and Brown 1993, Gotceitas et al. 1995, Persson and Eklov 1995, Tupper and Boutilier 1995, Gotceitas et al. 1997, Rangeley and Kramer 1998, Linehan et al. 2001, Heck et al. 2003, Laurel et al. 2003a). Predator foraging is at a disadvantage in structure as a result of decreased visual and swimming abilities (Crowder and Cooper 1982, Savino and Stein 1982, Matilla 1992).

In this study, I also examined the use of concealed and motionless behaviours as anti-predator strategies. Initial exposure to a predator usually results in hiding, freezing, or aggregating (Sih 1979). There was little difference in the behavioural trends (i.e. concealed and motionless behaviours) of white hake and Greenland cod during predator exposure in the intraspecific experiments. However, during the interspecific experiments, white hake spent significantly more time concealed than Greenland cod during exposure to the active predator and significantly more time motionless during exposure to both predator types. It is possible that the different anti-predator strategies are a reflection of the morphological differences between these two species (Scott and Scott 1988, Pitcher and Alheit 1995).

There are two types of swimming that are commonly referred to: "burst" and "continuous" (Blake 1983), and different morphological characteristics are associated with each: robust and streamlined, respectively. White hake body characteristics are more robust relative to Greenland cod, which is more streamlined due to its posterior compression. The difference in body shape suggests that Greenland cod are more mobile, selecting for a lifestyle that involves more continuous swimming. In contrast, hake are ambush predators (Pitcher and Alheit 1995), suggesting a more sedentary lifestyle than Greenland cod. This more sedentary way of life might allow white hake to remain more inconspicuous to predators than Greenland cod, even in barren substrates.

When juvenile white hake and Greenland cod overlapped spatially and temporally in the same tank, habitat use by cod was inconsistent prior to predator exposure. When exposed to a passive predator, cod used cobble significantly less and

sand significantly more than hake. When exposed to an active predator, Greenland cod used eelgrass significantly less and sand significantly more than hake. During the interspecific experiment cod consistently spent more time than hake above the sand substrate, which is a high risk habitat (Laurel et al. 2004). These results suggested that habitat use by juvenile Greenland cod may have been partially driven by avoidance of white hake. Moreover, because both the passive and active predators showed no habitat preference it is highly likely that juvenile white hake were a main factor influencing Greenland cod habitat use during predator exposure. Alternatively, cod may have moved into the sand habitat to see the predator better or to maximize their distance from the predator.

It is also likely that Greenland cod spent more time in the riskier habitat than white hake due to the influence that body size has on the outcome of competition (Abbot et al. 1985, Wazlavek and Figler 1989, Sabo and Pauley 1997). At the time of the experiment, the juvenile white hake were on average 1.45 times longer than the cod. This size difference is a natural phenomenon that is a result of high hake growth rates during their first year (Markle et al. 1982, Fahay and Able 1989, Lang et al. 1996, Able and Fahay 1998). White hake have a "get big quick" life history strategy (Markle et al. 1982), which results in juvenile white hake having a noticeable size advantage over Greenland cod right from the day that these two species settle to the demersal life stage (Ings 2005). In coastal Newfoundland, any size advantage seen is important because hake and cod settle to the demersal life stage at approximately the same time, and when settlement time does differ, hake almost invariably settle first (Laurel et al. submitted).

The "bigger is better" hypothesis implies that large body size and rapid growth during larval and juvenile stages leads to enhanced survival (Sogard 1997). Survival probability usually increases with size because larger individuals should tolerate physiological extremes, resist starvation, and attain a size refuge from predation sooner than smaller individuals (Sogard 1997). Although, this hypothesis generally refers to members of the same cohort (Sogard 1997), it is possible to expand the premises to interspecific relations, specifically those that involve co-occuring larval and juvenile fish. Thus, the habitat use of juvenile white hake supports the "bigger is better" hypothesis (Sogard 1997).

The much higher growth rate of juvenile white hake compared to Greenland cod resulted in a 1.45 times size difference in this experiment. Thus, white hake were almost large enough to prey on their co-habitants. Moreover, as hake grow they become increasingly piscivorous (Garrison and Link 2000) and as size-selective foragers (Coates et al. 1982), with a relatively large gape-size it is extremely likely that first year white hake do feed on Greenland cod at some point during the demersal juvenile stage. However, the minimum predator-prey ratio for piscivores is typically 2:1 (Power 1987, Miller et al. 1988). This suggests that the few observed agonistic behaviours shown by white hake in my experiments were more likely an expression of competition than attempted predation. However, the competitive edge that juvenile white hake appear to have over Greenland cod might have been strengthened if cod felt threatened by hake as a result of predation risk.

Juvenile white hake are not only likely to negatively impact Greenland cod, but also juveniles of its sister species, the Atlantic cod (*G. morhua*), which overlaps

spatially and temporally with both species in coastal Newfoundland (Laurel et al. submitted). The negative correlation found in the past decade between juvenile white hake and Atlantic cod densities on the northeast coast of Newfoundland (Laurel et al. submitted) supports this contention. All three species of gadids appear to prefer to settle in eelgrass (Laurel et al. submitted). Given that juvenile Atlantic cod have relatively slow growth rates compared to white hake and the fact that they settle demersally after white hake and Greenland cod in coastal Newfoundland, it is quite possible that the negative effects that hake have on Greenland cod habitat use might be at least severe, if not more so on Atlantic cod. Negative community interactions such as competition can slow the recovery of an overfished species (Baskett et al. 2006) and therefore, interactions with high densities of white hake may be limiting Atlantic cod recovery to some degree.

The "cultivation hypothesis" (Walters and Kitchell 2001) states that in order to remain dominant, top predators need to continue acquiring trophic resources and ensure the best trophic conditions for juvenile conspecifics. This hypothesis may be directly applied to the northern Atlantic cod stock, which collapsed in the early 1990's (Taggart et al. 1994). If the "cultivation hypothesis" holds for this example, there should be substantial population increases of competitors and predators of juvenile Atlantic cod in their preferred nursery areas after fishery induced collapse (Walters and Kitchell 2001). This is one possible explanation for the increasing abundance of juvenile white hake density in Newman Sound, Newfoundland. The "cultivation hypothesis" suggests that adult Atlantic cod are no longer able to regulate the expansion of other juvenile species into nursery areas where Atlantic cod

juveniles were once dominant. If Atlantic cod continually fails to recover, the area where young cod are found might continue to decrease, resulting in increased vulnerability to fishing and predation (Blanchard et al. 2005).

The strength of my study is that I could control variables that are not easily controlled in the field. Laboratory studies also generate new questions. Future research on this topic should determine how stem density of eelgrass affects habitat use by juvenile white hake and Greenland cod. It is well known that eelgrass structure varies in density and patchiness (Robbins and Bell 1994). Furthermore, future research on this topic would be benefited by using more replicate predators. In this experiment I statistically tested for and found differences in predator activity levels. As a result, I was able to suggest, but not conclude that behavioural differences among the predators in my experiment were responsible for differential behaviours and habitat use of juvenile fish.

To surmise, my study shows that juvenile white hake and Greenland cod adopt different anti-predator behaviours, which may in turn influence their interactions. The more sedentary lifestyle of juvenile white hake may lead them to remain concealed and motionless until danger seems imminent, at which time they use "burst" swimming to escape predation. In contrast, qualitative observations suggest that the more mobile lifestyle of Greenland cod may lead them to simply keep a greater distance from potential predators, including juvenile white hake (C.W. Lewis, pers. obs.), especially considering that predation is a main driving force behind habitat selection.

My study also documents experimentally overlapping habitat use by juvenile white hake and Greenland cod and supports the contention that eelgrass serves as an important nursery habitat for both species. In nature, there is a fine line between predation and competition and in my study in particular, predation is the ultimate form of competition. Because no predation on Greenland cod by white hake was observed throughout my study, I attributed my findings to be a result of habitat competition. Therefore, the evidence of habitat competition by white hake during interspecific interactions suggests that hake have the ability to push Greenland cod out of preferred habitat during high risk situations. As a result, Greenland cod spent more time over sand substrates than white hake and in aquatic ecosystems this is a bad thing because the odds of being preyed upon by a predator increase in habitats that lack cover or structure.

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CHAPTER 3

Summary, Conclusions, and Future Work

My study provides evidence to support the nursery role hypothesis that eelgrass is thought to play. Other studies on juvenile gadids in coastal Newfoundland have also supported this contention (eg. Gotceitas et al. 1997, Linehan et al. 2001, Laurel et al. 2003). My study shows specifically that juvenile Greenland cod (*Gadus ogac*) have a high affinity for eelgrass habitat, whereas white hake (*Urophycis tenuis*) appear to select habitat based on structural complexity. These habitat use patterns are especially evident during intraspecific situations. Furthermore, comparable observations have been made in Newman Sound, Newfoundland (Gregory and Laurel unpublished data).

Based on the similar use of habitat by juvenile white hake and Greenland cod I assumed the potential for habitat competition to be high. Evidence to support this premise was seen during interspecific situations, when both species co-occurred in a laboratory setting. I found that exposure to passive and active predators under these conditions caused cod to use cobble and eelgrass significantly less than hake, respectively. Additionally, exposure to both predator types resulted in cod using sand significantly more. The resulting interactions suggested that white hake were able to prevent Greenland cod from using safer, complex habitats during dangerous situations. Therefore, since the abundance of white hake on the northeast coast of Newfoundland has been increasing, especially in the past few years (Laurel et al. submitted), it is quite possible that hake are negatively impacting Greenland cod.

Moreover, during years when habitat use is more likely to be density dependent, Greenland cod are less flexible to using alternate habitats (Laurel et al. 2004).

The use of sub-optimal habitat by Greenland cod when co-habiting with white hake during risk of predation is further complicated by the rapid growth rates seen in young of the year white hake (Markle et al. 1982, Fahay and Able 1989, Lang et al. 1996, Able and Fahay 1998). Even though white hake and Greenland cod usually settle to the demersal lifestage concurrently in mid to late July on the northeast coast of Newfoundland (Ings 2005), a noticeable size difference can be seen as early as September in the same year (Thistle 2006). Agonistic behaviours displayed by white hake may further impede juvenile Greenland cod from using their favoured habitat. In my study, during interspecific situations I observed white hake chasing other co-existing fish; a behaviour that was not seen in Greenland cod.

During my study I also observed differences in anti-predator behaviours between these two species. White hake tended to use concealed and motionless behaviours moreso than Greenland cod during predator exposure in an interspecific setting; in contrast Greenland cod spent more time swimming. It is possible that the different anti-predator strategies were a reflection of the morphological differences between these two species (Scott and Scott 1988, Pitcher and Alheit 1995). The more sedentary lifestyle of juvenile white hake may cause them to remain concealed and motionless until danger seems imminent, at which time they use "burst" swimming to escape predation. In contrast, the more mobile lifestyle of Greenland cod may lead them to simply keep a greater distance from potential predators.

My research is one of the first behavioural studies to shed light on how interactions between juvenile white hake and Greenland cod affect their use of habitat. Studies such as this one are important, because research on the habitat use and nursery requirements of juvenile fish play major roles in the successful management of fish populations (Langton et al. 1996, COSEWIC 2003, Cote et al. 2004). Especially important, are studies that examine how commercially valuable fish are affected by other co-existing species. Since juvenile Atlantic cod (*G. morhua*) co-occurs with white hake and Greenland cod in coastal Newfoundland (Laurel et al. submitted), future research should concentrate on interactions among all three of these species. By studying the interactions of all three species, knowledge of juvenile Atlantic cod could be increased and insight as to why the Northern Atlantic cod stocks continually fail to recover could be gained.

In conclusion, my work suggests that in areas where white hake and Greenland cod co-habit as demersal juveniles habitat competition is likely to occur. The outcome of habitat competition between these two species should result in juvenile Greenland cod using sub-optimal, less complex habitats, especially in years where high densities of white hake settle to nearshore areas of Newfoundland. The effects of juvenile white hake, a species near the northern extent of its range, on Greenland cod, a species near the southern extent of its range, should be monitored closely, especially since interactions between these two species are relatively new. In addition, since juvenile white hake have only recently become numerically abundant on the northeast coast of Newfoundland and because there has been a negative correlation found in the past decade between juvenile white hake and Atlantic cod

densities in Newman Sound (Laurel et al. submitted), future research should also look at interactions between these two species.

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APPENDIX A. Summary of observations made on each juvenile white hake during the intraspecific competition experiment. Note: Time effect was eliminated and all observations made on an individual fish were averaged for each predator treatment.

Abbreviations	
PT	predator treatment
Conc	time concealed
Open	time in open
Mov	time moving
Mot	time motionless
EG	time in/above eelgrass
CO	time in/above cobble
SA	time above sand
Chse	# of chases
Flees	# of flees

predator treatment	
B	before exposure
D	during exposure
A	after exposure

Fish #	PT	Conc (s)	Open (s)	Mov (s)	Mot (s)	EG (s)	CO (s)	SA (s)	Chse	Flees
1	B	0.00	120.00	96.95	13.25	24.92	47.52	47.57	2	4
2	B	54.22	65.78	68.15	51.18	68.47	21.52	30.02	0	2
3	B	100.00	20.00	20.00	100.00	104.72	0.00	15.28	0	2
4	B	83.12	36.88	41.70	78.30	93.42	6.00	20.58	0	2
5	B	89.78	30.22	39.60	80.40	9.40	107.04	3.56	0	0
6	B	95.83	24.17	37.08	82.92	112.52	7.48	0.00	0	0
7	B	0.00	120.00	115.15	0.00	35.67	17.40	66.93	0	1
8	B	116.07	3.93	32.38	87.62	116.47	0.00	3.53	0	1
9	B	0.00	120.00	110.38	0.00	50.00	62.95	7.05	0	2
10	B	0.00	120.00	118.27	0.00	26.63	73.53	19.83	0	8
11	B	60.17	59.83	60.00	60.00	75.85	0.67	43.48	1	1
12	B	12.18	107.82	119.03	0.97	41.28	43.63	35.08	0	4
13	B	2.80	117.20	120.00	0.00	43.78	50.92	25.30	2	5
14	B	16.37	103.63	86.30	33.70	10.62	64.95	44.43	0	5
15	B	53.33	66.67	79.85	40.15	105.55	0.98	13.47	0	0
16	B	6.88	113.12	120.00	0.00	30.95	81.60	7.45	1	1
17	B	27.15	92.85	96.53	22.12	32.07	75.67	12.27	0	2
18	B	1.90	118.10	120.00	0.00	3.44	96.20	20.36	0	0
19	B	23.53	96.47	102.28	17.72	68.78	7.75	43.47	0	4
20	B	20.00	100.00	96.33	23.67	0.00	78.57	41.43	0	2
21	B	19.56	100.44	115.52	4.48	27.48	80.66	11.86	4	2
22	B	105.05	14.95	33.12	86.88	40.00	76.88	3.12	0	1
23	B	14.35	105.65	120.00	0.00	51.13	22.90	45.97	0	1
24	B	15.53	104.47	108.25	11.75	42.03	46.52	31.45	2	3
25	B	20.00	100.00	81.15	32.55	0.00	84.23	35.77	0	1
26	B	1.05	118.95	120.00	0.00	33.08	58.35	28.57	2	1

27	B	29.83	90.17	86.28	33.72	102.42	0.00	17.58	0	2
28	B	2.22	117.78	119.52	0.48	6.52	75.40	38.08	1	5
29	B	8.28	111.72	120.00	0.00	10.26	93.30	16.44	0	1
30	B	60.00	60.00	43.70	76.30	62.12	6.83	51.05	1	3
31	B	23.35	96.65	114.15	2.98	91.92	20.42	7.67	1	1
32	B	0.00	120.00	120.00	0.00	44.67	40.77	34.57	1	0
1	D	20.00	100.00	51.28	27.57	27.15	35.07	57.78	0	3
2	D	99.86	20.14	18.60	53.03	99.70	8.66	11.64	0	1
3	D	20.00	100.00	88.12	20.00	20.45	68.45	31.10	0	6
4	D	33.57	86.43	98.92	20.00	2.82	110.70	6.48	0	12
5	D	100.53	19.47	13.10	106.90	100.65	0.00	19.35	0	4
6	D	103.82	16.18	17.23	100.40	100.00	16.85	3.15	0	0
7	D	0.00	120.00	114.50	0.00	0.00	29.52	90.48	0	6
8	D	109.27	10.73	20.00	100.00	105.25	8.68	6.07	0	5
9	D	80.00	40.00	26.85	80.25	98.82	15.23	5.95	0	1
10	D	28.32	91.68	65.28	20.92	58.82	54.57	6.62	0	0
11	D	21.65	98.35	70.43	21.20	22.32	63.15	34.53	0	5
12	D	5.82	114.18	113.73	4.35	1.07	102.93	16.00	5	3
13	D	118.57	1.43	16.22	103.78	119.47	0.00	0.53	0	0
14	D	100.00	20.00	21.87	98.13	114.45	0.00	5.55	0	0
15	D	20.00	100.00	81.60	6.40	22.67	3.22	94.12	0	8
16	D	0.00	120.00	119.52	0.48	19.82	21.80	78.38	0	5
17	D	63.60	56.40	31.90	83.45	68.15	4.83	47.02	0	2
18	D	40.67	79.33	71.65	0.00	39.52	68.38	12.10	1	0
19	D	2.75	117.25	88.35	10.93	2.67	69.32	48.02	0	3
20	D	36.37	83.63	97.15	22.85	16.70	95.93	7.37	0	3
21	D	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
22	D	108.83	11.17	20.63	99.37	103.77	11.67	4.57	1	2
23	D	7.05	112.95	120.00	0.00	5.90	18.35	95.75	0	0
24	D	0.00	120.00	118.62	0.00	0.00	15.57	104.43	0	1
25	D	0.00	120.00	68.43	22.97	5.77	41.27	72.97	0	5
26	D	69.94	50.06	46.38	11.04	87.98	24.82	7.20	0	0
27	D	5.05	114.95	65.42	36.18	5.40	52.37	62.23	0	5
28	D	9.40	110.60	117.32	2.68	0.00	94.75	25.25	2	10
29	D	35.08	84.92	94.53	25.47	0.00	95.87	24.13	0	4
30	D	113.63	6.37	55.72	64.28	99.53	18.92	1.55	0	0
31	D	3.18	116.82	82.85	0.00	4.87	34.93	80.20	0	6
32	D	0.00	120.00	120.00	0.00	37.67	44.28	38.05	0	6
1	A	3.90	116.10	120.00	0.00	24.35	57.05	38.60	0	1
2	A	92.97	27.03	29.57	90.43	4.25	113.82	1.93	3	0
3	A	11.92	108.08	108.08	11.92	1.38	24.63	93.98	0	0
4	A	20.00	100.00	100.00	20.00	39.83	46.02	34.15	0	0
5	A	112.87	7.13	7.73	112.27	120.00	0.00	0.00	0	0
6	A	113.53	6.47	34.03	85.97	114.03	0.00	5.97	0	2
7	A	0.00	120.00	118.80	0.00	4.50	33.82	81.68	0	7
8	A	45.37	74.63	77.28	35.65	60.85	11.05	48.10	0	4
9	A	77.33	42.67	42.20	75.80	90.15	24.72	5.13	0	2
10	A	1.02	118.98	108.17	11.83	70.00	15.85	34.15	0	1

11	A	6.95	113.05	114.53	5.47	15.93	9.92	94.15	0	0
12	A	0.00	120.00	119.25	0.38	10.62	52.05	57.33	4	7
13	A	93.55	26.45	40.00	80.00	97.77	0.00	22.23	0	0
14	A	10.02	109.98	111.53	8.47	30.55	12.10	77.35	0	3
15	A	18.70	101.30	107.30	12.70	33.32	28.35	58.33	0	1
16	A	0.47	119.53	120.00	0.00	39.32	30.88	49.80	0	2
17	A	6.33	113.67	120.00	0.00	10.47	74.03	35.50	1	4
18	A	20.00	100.00	120.00	0.00	20.00	80.13	19.87	0	1
19	A	60.60	59.40	60.42	59.58	73.98	0.48	45.53	0	1
20	A	24.33	95.67	100.00	20.00	39.37	68.88	11.75	0	3
21	A	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
22	A	51.43	68.57	88.88	31.12	55.23	18.60	46.17	2	0
23	A	6.52	113.48	120.00	0.00	5.77	19.90	94.33	0	2
24	A	0.00	120.00	115.63	0.00	3.27	23.50	93.23	0	5
25	A	0.00	120.00	120.00	0.00	6.17	67.85	45.98	0	2
26	A	17.52	102.48	119.47	0.53	58.85	43.40	17.75	1	1
27	A	60.00	60.00	60.00	60.00	0.00	64.95	55.05	0	1
28	A	0.00	120.00	111.13	6.00	0.00	94.02	25.98	0	0
29	A	75.10	44.90	63.82	54.65	52.38	67.62	0.00	1	0
30	A	115.95	4.05	25.05	94.95	116.35	0.00	3.65	0	1
31	A	10.92	109.08	104.88	8.50	37.93	6.63	75.43	0	0
32	A	5.38	114.62	120.00	0.00	21.72	46.08	52.20	0	0

APPENDIX B. Summary of observations made on each juvenile Greenland cod during the intraspecific competition experiment. Note: Time effect was eliminated and all observations made on an individual fish were averaged for each predator treatment.

Abbreviations	
PT	predator treatment
Conc	time concealed
Open	time in open
Mov	time moving
Mot	time motionless
EG	time in/above eelgrass
CO	time in/above cobble
SA	time above sand
Chse	# of chases
Flees	# of flees

predator treatment	
B	before exposure
D	during exposure
A	after exposure

Fish #	PT	Conc (s)	Open (s)	Mov (s)	Mot (s)	EG (s)	CO (s)	SA (s)	Chse	Flees
1	B	102.17	17.83	34.00	78.33	103.92	6.23	9.85	0	0
2	B	6.05	113.95	63.53	56.47	13.43	6.57	100.00	0	0
3	B	37.27	82.73	99.47	20.53	58.00	18.53	43.47	0	0
4	B	82.47	37.53	63.20	43.52	113.05	4.37	2.58	0	1
5	B	120.00	0.00	70.17	41.07	33.40	85.15	1.45	0	0
6	B	52.82	67.18	99.48	20.52	44.78	28.75	46.47	2	0
7	B	41.45	78.55	70.88	49.12	28.98	68.67	22.35	0	0
8	B	98.03	21.97	39.52	78.40	100.93	4.83	14.23	1	0
9	B	39.40	80.60	95.97	6.62	15.67	85.85	18.48	0	0
10	B	110.93	9.07	21.92	98.08	111.30	7.47	1.23	1	0
11	B	0.00	120.00	73.40	46.60	0.00	120.00	0.00	0	0
12	B	50.80	69.20	93.58	26.42	18.52	81.67	19.82	0	0
13	B	40.00	80.00	81.93	38.07	0.00	60.00	60.00	0	0
14	B	120.00	0.00	12.98	107.02	120.00	0.00	0.00	0	0
15	B	11.38	108.62	116.32	3.68	34.97	11.00	74.03	0	0
16	B	87.93	32.07	53.03	66.97	99.27	20.73	0.00	0	0
17	B	119.64	0.36	21.66	94.02	120.00	0.00	0.00	0	0
18	B	118.35	1.65	18.00	102.00	116.93	3.07	0.00	0	0
19	B	88.58	31.42	82.67	37.33	92.20	0.00	27.80	0	0
20	B	118.43	1.57	7.85	109.50	120.00	0.00	0.00	0	0
21	B	72.17	47.83	63.63	56.37	51.90	68.10	0.00	0	0
22	B	95.87	24.13	41.05	78.95	29.18	70.82	20.00	0	0
23	B	71.30	48.70	90.95	28.35	29.25	84.50	6.25	0	2
24	B	70.22	49.78	86.60	33.40	70.87	11.77	37.37	0	3
25	B	17.85	102.15	72.88	47.12	11.72	0.00	108.28	0	0

26	B	106.67	13.33	30.53	89.47	0.00	120.00	0.00	0	0
27	B	86.58	33.42	59.73	60.27	87.28	15.80	16.92	0	0
28	B	5.62	114.38	96.05	12.25	20.68	99.32	0.00	0	0
29	B	120.00	0.00	6.97	113.03	100.00	20.00	0.00	0	0
30	B	120.00	0.00	3.63	116.37	120.00	0.00	0.00	0	0
31	B	109.95	10.05	20.20	96.93	112.62	7.38	0.00	0	1
32	B	5.55	114.45	112.23	1.37	8.72	28.85	82.43	2	0
1	D	118.08	1.92	0.53	0.00	117.95	2.05	0.00	0	0
2	D	9.77	110.23	69.28	22.68	9.50	6.50	104.00	0	5
3	D	13.27	106.73	77.00	0.00	62.83	57.17	0.00	0	0
4	D	72.42	47.58	54.33	45.67	55.25	64.75	0.00	0	1
5	D	36.65	83.35	55.23	14.00	65.08	0.38	54.53	0	4
6	D	5.32	114.68	76.32	1.05	7.68	57.73	54.58	0	2
7	D	102.92	17.08	17.53	89.02	103.63	16.37	0.00	0	5
8	D	28.73	91.27	43.93	20.37	81.37	12.58	26.05	0	0
9	D	81.53	38.47	28.92	0.00	93.73	15.35	10.92	0	7
10	D	30.37	89.63	57.67	20.00	33.42	10.03	76.55	0	2
11	D	104.60	15.40	6.25	113.75	114.03	4.45	1.52	0	4
12	D	110.25	9.75	55.08	52.40	64.83	49.32	5.85	0	1
13	D	67.58	52.42	62.48	31.76	74.02	2.82	43.16	0	1
14	D	10.72	109.28	40.73	2.77	14.48	45.02	60.50	0	1
15	D	102.08	17.92	26.22	87.53	120.00	0.00	0.00	0	3
16	D	32.23	87.77	67.08	5.12	76.48	37.70	5.82	1	0
17	D	102.17	17.83	20.00	17.37	107.78	0.00	12.22	0	1
18	D	28.73	91.27	48.25	39.57	38.30	3.78	77.92	0	1
19	D	21.05	98.95	85.02	0.82	31.10	88.38	0.52	0	4
20	D	118.66	1.34	9.12	110.88	71.26	48.74	0.00	0	0
21	D	43.64	76.36	27.42	45.00	42.92	25.28	51.80	0	3
22	D	0.47	119.53	35.87	0.00	6.85	59.28	53.87	0	5
23	D	102.00	18.00	30.08	89.92	102.13	17.87	0.00	0	4
24	D	31.18	88.82	52.07	20.00	92.30	10.95	16.75	0	0
25	D	97.12	22.88	14.80	0.00	105.17	1.40	13.43	0	4
26	D	113.43	6.57	6.40	113.60	0.00	119.40	0.60	0	0
27	D	0.52	119.48	70.00	0.00	23.48	83.78	12.73	0	0
28	D	45.47	74.53	65.80	45.15	35.85	81.40	2.75	0	2
29	D	68.28	51.72	25.88	24.13	71.78	20.00	28.22	0	1
30	D	7.47	112.53	50.05	2.55	13.97	26.83	79.20	0	2
31	D	117.22	2.78	14.48	101.25	118.08	0.00	1.92	0	0
32	D	50.73	69.27	27.90	28.55	101.92	4.72	13.37	0	2
1	A	0.00	120.00	7.08	20.00	0.28	112.75	6.97	0	0
2	A	27.05	92.95	115.80	4.20	28.20	0.00	91.80	0	1
3	A	42.47	77.53	114.38	5.62	114.68	5.32	0.00	0	0
4	A	50.70	69.30	70.90	8.13	90.58	27.92	1.50	0	0
5	A	78.43	41.57	89.03	26.28	80.77	33.35	5.88	0	0
6	A	19.25	100.75	120.00	0.00	67.70	47.23	5.07	0	0
7	A	59.58	60.42	45.70	74.30	2.83	83.05	34.12	1	0
8	A	70.67	49.33	27.73	60.00	82.82	9.47	27.72	0	0
9	A	7.40	112.60	51.00	3.03	14.97	101.87	3.17	0	0

10	A	95.65	24.35	41.17	78.83	108.53	7.28	4.18	0	0
11	A	76.70	43.30	48.95	71.05	1.87	116.25	1.88	0	0
12	A	81.28	38.72	37.74	82.26	34.60	48.00	37.40	0	0
13	A	77.65	42.35	97.88	0.00	29.27	74.82	15.92	0	0
14	A	115.62	4.38	20.00	100.00	118.45	0.00	1.55	0	0
15	A	7.87	112.13	120.00	0.00	18.18	1.97	99.85	0	2
16	A	45.15	74.90	73.13	3.15	66.08	23.43	30.48	0	0
17	A	0.00	120.00	32.25	2.53	13.48	93.12	13.40	0	0
18	A	111.82	8.18	39.58	80.42	116.70	2.52	0.78	0	1
19	A	61.63	58.37	65.97	54.03	61.95	10.28	47.77	0	1
20	A	41.83	78.17	63.22	29.12	82.33	24.27	13.40	0	0
21	A	87.85	32.15	20.30	80.00	84.22	35.78	0.00	0	0
22	A	112.04	7.96	47.98	72.02	0.00	120.00	0.00	1	0
23	A	71.38	48.62	90.98	28.92	95.08	20.53	4.38	0	0
24	A	30.38	89.62	110.70	0.00	52.87	22.85	44.28	0	0
25	A	20.60	99.40	103.30	0.73	59.88	38.73	21.38	0	0
26	A	96.42	23.58	31.10	80.00	40.08	63.50	16.42	1	0
27	A	88.92	31.08	66.40	53.60	97.00	0.00	23.00	0	0
28	A	0.80	119.20	63.14	0.00	60.20	52.20	7.60	0	1
29	A	89.07	30.93	49.53	60.17	55.03	50.40	14.57	0	0
30	A	100.00	20.00	21.33	98.67	102.95	0.00	17.05	0	1
31	A	90.52	29.48	40.30	79.70	110.42	9.58	0.00	0	1
32	A	29.90	90.10	68.97	21.00	68.80	1.62	49.58	0	0

APPENDIX C. Summary of observations made on each juvenile fish during the interspecific competition experiment. Note: Time effect was eliminated and all observations made on an individual fish were averaged for each predator treatment.

Abbreviations	
Sp	juvenile species
PT	predator treatment
P	predator type
Conc	time concealed
Open	time in open
Mov	time moving
Mot	time motionless
EG	time in/above eelgrass
CO	time in/above cobble
SA	time above sand
Chse	# of chases
Flees	# of flees

juvenile species	
GC	Greenland cod
WH	white hake
predator treatment	
B	before exposure
D	during exposure
A	after exposure
predator type	
A	active
P	passive
N	none

Fish #	Sp	PT	P	Conc (s)	Open (s)	Mov (s)	Mot (s)	EG (s)	CO (s)	SA (s)	Chse	Flees
1	WH	B	N	120.00	0.00	3.42	116.58	120.00	0.00	0.00	0	0
6	WH	B	N	96.95	23.05	24.58	93.50	100.00	4.27	15.73	2	0
8	WH	B	N	0.00	120.00	120.00	0.00	0.00	88.42	31.58	1	0
13	WH	B	N	59.88	60.12	75.43	44.57	87.35	32.65	0.00	0	0
22	WH	B	N	107.63	12.37	16.42	103.58	0.57	113.77	5.67	0	1
24	WH	B	N	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
26	WH	B	N	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
29	WH	B	N	20.00	100.00	41.13	66.87	0.00	51.52	68.48	1	2
5	WH	B	N	78.80	41.20	55.22	64.78	76.42	35.57	8.02	3	0
7	WH	B	N	104.18	15.82	17.53	102.47	60.00	47.40	12.60	0	0
12	WH	B	N	60.00	60.00	27.02	92.98	65.17	2.23	52.60	1	0
14	WH	B	N	120.00	0.00	0.00	120.00	0.00	120.00	0.00	0	0
17	WH	B	N	81.93	38.07	58.47	61.53	51.55	52.40	16.05	0	5
19	WH	B	N	119.08	0.92	1.07	118.93	100.00	20.00	0.00	0	0
25	WH	B	N	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
28	WH	B	N	53.60	66.40	72.02	47.98	4.47	81.43	34.10	2	3
1	WH	D	A	120.00	0.00	0.00	120.00	100.00	20.00	0.00	0	0

6	WH	D	A	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
8	WH	D	A	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
13	WH	D	A	20.00	100.00	100.00	20.00	3.30	111.87	4.83	0	6
22	WH	D	A	1.78	118.22	100.00	20.00	23.47	8.22	88.32	0	11
24	WH	D	A	64.03	55.97	72.35	47.65	65.80	23.32	30.88	0	0
26	WH	D	A	120.00	0.00	0.00	120.00	0.00	120.00	0.00	0	0
29	WH	D	A	0.00	120.00	120.00	0.00	0.03	109.37	10.60	0	11
5	WH	D	P	49.08	70.92	61.85	29.75	17.57	91.75	10.68	0	3
7	WH	D	P	40.00	80.00	62.03	57.97	11.52	84.25	24.23	2	0
12	WH	D	P	80.00	40.00	29.03	90.97	96.95	0.65	22.40	0	0
14	WH	D	P	83.98	36.02	55.78	64.22	12.42	100.35	7.23	0	4
17	WH	D	P	55.52	64.48	82.90	24.57	2.32	113.73	3.95	1	0
19	WH	D	P	73.03	46.97	27.70	92.30	67.52	26.23	26.25	0	0
25	WH	D	P	78.95	41.05	54.67	65.33	26.67	90.93	2.40	0	1
28	WH	D	P	75.25	44.75	78.02	41.98	3.87	97.60	18.53	1	1
1	WH	A	N	120.00	0.00	0.00	120.00	120.00	0.00	0.00	0	0
6	WH	A	N	38.08	81.92	89.68	30.32	15.35	66.15	38.50	2	0
8	WH	A	N	100.00	20.00	20.00	100.00	113.03	1.80	5.17	0	0
13	WH	A	N	0.00	120.00	119.25	0.00	7.73	108.27	4.00	0	0
22	WH	A	N	29.47	90.53	94.35	25.65	57.55	16.57	45.88	1	3
24	WH	A	N	88.30	31.70	34.45	85.55	88.65	10.72	20.63	0	2
26	WH	A	N	100.00	20.00	0.17	119.83	0.00	100.00	20.00	0	0
29	WH	A	N	11.23	108.77	117.95	2.05	0.00	90.08	29.92	0	2
5	WH	A	N	112.65	7.35	20.00	100.00	102.57	17.43	0.00	0	0
7	WH	A	N	80.00	40.00	3.45	116.55	40.00	59.58	20.42	0	0
12	WH	A	N	80.00	40.00	0.00	120.00	80.00	0.00	40.00	0	0
14	WH	A	N	95.55	24.45	10.92	109.08	0.00	120.00	0.00	0	0
17	WH	A	N	117.65	2.35	23.88	96.12	0.22	119.78	0.00	1	0
19	WH	A	N	120.00	0.00	13.07	106.93	117.82	0.00	2.18	0	0
25	WH	A	N	65.50	54.50	54.45	65.55	12.13	84.77	23.10	1	0
28	WH	A	N	46.97	73.03	78.82	41.18	2.80	79.78	37.42	0	0
3	GC	B	N	51.58	68.42	86.93	32.67	53.77	21.60	44.63	0	6
10	GC	B	N	1.02	118.98	120.00	0.00	17.05	35.27	67.68	0	3
16	GC	B	N	85.85	34.15	60.28	59.72	0.00	118.03	1.97	0	0
18	GC	B	N	120.00	0.00	24.48	95.52	22.38	97.62	0.00	0	0
21	GC	B	N	120.00	0.00	18.03	101.97	109.37	10.63	0.00	0	0
27	GC	B	N	102.75	17.25	94.07	25.93	2.60	100.00	17.40	0	1
30	GC	B	N	73.22	46.78	80.00	40.00	18.93	95.07	6.00	0	0
31	GC	B	N	0.00	120.00	114.92	2.10	6.18	0.15	113.67	0	1
2	GC	B	N	24.00	96.00	69.02	50.98	53.06	3.56	63.38	0	0
4	GC	B	N	38.70	81.30	115.52	4.48	32.72	61.78	25.50	0	2
9	GC	B	N	74.80	45.20	47.70	72.30	99.40	0.00	20.60	0	0
11	GC	B	N	109.05	10.95	51.57	68.43	110.20	0.00	9.80	0	0
15	GC	B	N	13.02	106.98	116.67	3.33	13.05	3.45	103.50	0	2
20	GC	B	N	98.87	21.13	38.79	81.21	89.37	8.90	21.73	0	0
23	GC	B	N	96.50	23.50	43.07	76.93	53.08	48.70	18.22	0	0
32	GC	B	N	99.23	20.77	40.00	80.00	101.68	18.32	0.00	0	0
3	GC	D	A	0.00	120.00	54.43	1.82	2.28	2.20	115.52	0	3

10	GC	D	A	1.70	118.30	120.00	0.00	16.57	44.13	59.30	0	4
16	GC	D	A	120.00	0.00	9.43	110.57	0.60	119.40	0.00	0	0
18	GC	D	A	18.38	101.62	110.33	5.85	28.53	5.75	85.72	0	7
21	GC	D	A	96.20	23.80	51.67	68.33	44.38	60.97	14.65	0	2
27	GC	D	A	8.78	111.22	68.43	3.00	2.38	8.12	109.50	0	4
30	GC	D	A	80.00	40.00	55.05	64.95	94.03	0.00	25.97	0	1
31	GC	D	A	0.00	120.00	120.00	0.00	8.65	82.22	29.13	0	4
2	GC	D	P	0.47	119.53	116.30	0.00	82.12	28.23	9.65	0	1
4	GC	D	P	51.08	68.92	120.00	0.00	35.62	59.25	25.13	0	4
9	GC	D	P	0.00	120.00	90.15	0.00	70.78	0.00	49.22	0	1
11	GC	D	P	55.62	64.38	75.63	40.38	13.75	83.12	23.13	0	4
15	GC	D	P	20.00	100.00	100.43	19.57	27.27	6.58	86.15	0	4
20	GC	D	P	36.25	83.75	97.37	21.93	27.45	59.12	33.43	0	3
23	GC	D	P	33.63	86.37	74.17	24.90	37.53	5.20	77.27	0	0
32	GC	D	P	0.00	120.00	98.20	0.00	35.62	50.42	33.97	0	1
3	GC	A	N	18.78	101.22	95.72	4.28	25.60	20.70	73.70	0	2
10	GC	A	N	2.92	117.08	116.70	3.30	21.37	31.70	66.93	0	0
16	GC	A	N	19.15	100.85	41.90	78.10	0.00	39.62	80.38	1	0
18	GC	A	N	118.68	1.32	10.10	109.90	118.80	0.00	1.20	0	0
21	GC	A	N	97.35	22.65	48.48	69.52	108.85	4.92	6.23	0	0
27	GC	A	N	0.00	120.00	99.28	0.00	1.55	0.30	118.15	0	2
30	GC	A	N	30.88	89.12	100.00	20.00	20.00	79.12	20.88	0	0
31	GC	A	N	80.00	40.00	40.90	79.10	86.18	0.00	33.82	0	0
2	GC	A	N	3.10	116.90	104.00	16.00	40.98	25.67	53.35	0	2
4	GC	A	N	13.95	106.05	116.27	0.00	15.17	57.48	47.35	0	0
9	GC	A	N	11.88	108.12	55.08	0.52	89.05	0.00	30.95	0	0
11	GC	A	N	118.50	1.50	9.55	110.45	120.00	0.00	0.00	0	0
15	GC	A	N	42.03	77.97	84.87	35.13	46.50	10.72	62.78	0	1
20	GC	A	N	96.45	23.55	48.48	71.52	88.25	16.68	15.07	0	0
23	GC	A	N	34.93	85.07	56.23	27.07	93.03	0.00	26.97	0	1
32	GC	A	N	93.53	26.47	46.83	73.17	99.28	13.33	7.38	0	0